Bat community structure and habitat use across logging regimes in jarrah eucalypt forests of south-western Australia

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Abstract

In many parts of the world, the increasing demand for timber and other forest products has led to loss, fragmentation, degradation or modification of natural forest habitats. The consequences of such habitat changes have been well studied for some animal groups, however not much is known of their effects on bats. In Australia, logging of native forests is a major threat to the continent's biodiversity and while logging practices have undergone great changes in the past three decades to selective logging (including ecologically sustainable forest management), which is more sympathetic to wildlife, there is still concern about the effects of logging on the habitat of many forest-dwelling animals. The goal of this thesis was to investigate the effects of logging on the bat species assemblages at both community and individual species levels in terms of their foraging and roosting ecology in jarrah forests of south-western Australia. This information is necessary to strengthen the scientific basis for ecologically sustainable forest management in production forests. The outcome of this research may help in the formulation of policy and management decisions to ensure the long-term maintenance and survival of viable populations of forest-dwelling bats in these altered environments. Bats were selected because they comprise more than 25% of Australia's mammal species and constitute a major component of Australia's biodiversity. In addition, bats play key roles in forest dynamics and may act as indicators of disturbance. In the jarrah forests, bats are a significant proportion of the mammal fauna (9 of around 30 native extant species).

As a basis of understanding how bats use modified habitats, nine species of bats were investigated by assessing their foraging and commuting habits (measured as bat

activity) in different forest types (logged, young regrowth and old regrowth forest). To assess patterns of habitat use across a gradient of managed forest conditions, and to help predict impacts of logging on bats, four replicates were selected from each of three distinct post-harvest management treatments, recently logged forest or gaps (<6 years since logging), young regrowth forest (12–30 years since logging) and old regrowth forest (> 30 years old). Sites were monitored for bat activity on two nights, with Anabat detectors placed on track and off-track positions. The relationships between bat species assemblages in terms of their relative use and foraging activity and various forest structural variables, and the relationship between bats and the insect biomass were examined in order to identify the effects on the bat fauna of historical logging practices. Overall, 12 sites were sampled (four sites for each forest type) with bat activity and vegetation structure conducted on-track and off-track at each site and insect abundance sampled only at off-track sites.

Secondly, because roosts are an important resource for bats, and may be a limiting factor in modified landscapes, we investigated the roosting requirements of two sympatric species of jarrah forest-dwelling vespertilionid bats, the Southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi*. Their sensitivity to the loss of roost sites from logging and the effectiveness of current management practices at conserving appropriate roost sites were examined. As part of the research, tree (age, size, type, condition, presence of hollows, loose bark) and landscape characteristics (elevation, logging history, distance to water holes and creeklines, etc) of roosting sites were compared with random trees and their surrounding forest structure at local roost tree and broader landscape scales to determine whether bats selected roost trees and sites with particular characteristics.

The fieldwork was carried out during 2007 – 2009 and information was gathered through capture, radiotelemetry and passive monitoring using echolocation call detectors. Specifically, harp traps and radiotelemetry were used for roost-selection studies while Anabat bat detectors were used to assess bat activity (commuting, foraging) among different logging histories and in response to forest structural attributes and insect activity. Light traps were used to assess insect availability in relation to bat activity and forest structure.

The activity of different bat species related in different ways to the structural vegetation parameters, generally reflecting bat echolocation ability and manoeuvrability. Bats tended to use tracks more than off-track locations, thereby avoiding clutter at off-track locations. At the same time, tracks recorded similar activity across logging histories. However, off-track activity in old regrowth was significantly greater than either young regrowth or recently logged forest. Two taxa, *Vespadelus regulus* and *Nyctophilus* spp. were more active in old regrowth than other logging histories. Similarly, *V. regulus*, *Nyctophilus* spp., *Chalinolobus gouldii*, *C. morio* and *Falsistrellus mackenziei* activity was significantly greater on-track than off-track, but this activity was similar on-track across forest types, suggesting bats' use of forest tracks was unaffected by logging. As an indication of the association of low bat activity off-track with clutter, negative relationships of under-storey clutter were the most consistent predictors of bat habitat use. Conversely, reduced clutter and abundant roost resources seemed the most likely explanations for greater activity at old regrowth sites.

There were both inter-specific similarities and differences in the selection and location of roost trees and roost sites between *V. regulus* and *N. gouldi*. Both species were highly selective, preferring old large trees (> 80 cm diameter at breast height over bark – DBHOB) at intermediate or advanced stages of decay, crown senescence and deterioration with a lower percent bark cover compared to random trees. Both species also selected hollows for roosting, with *V. regulus* roosting exclusively in hollows but a few *N. gouldi* also used roosts under decorticating bark, cracks and under balga (*Xanthorrhoea preissii*) skirts. *V. regulus* preferred tall trees in the canopy with roost entrances high above the ground with little surrounding vegetation while *N. gouldi* preferred roosting closer to the ground and in dense clutter. In general, little evidence was found of bats roosting in either shelterwood creation or gap release silvicultural treatments, although a few *N. gouldi* bats roosted in retained habitat, or remnant, trees in these silvicultural treatments. Only riparian buffers and structurally mature forests appeared to provide multiple alternate roosts, containing a higher density of trees with hollows required by bats for roosting. In contrast, gap release and shelterwood creation sites contained substantially lower densities of hollow bearing trees. Pockets of mature forest that were previously only lightly and selectively logged before the introduction of Ecologically Sustainable Forest Management (ESFM) were important roosting sites for bats. However, although some *N. gouldi* bats selected roosts in retained or remnant trees in gap release and shelterwood creation silvicultural treatments, it remains unclear if bats can successfully breed in such regrowth forests in the absence of older forest stands and this should be a priority for future studies.

This study demonstrated that unharvested buffer strips surrounding ephemeral streams, and more open mature forests, with reduced midstoreys, were important roosting habitats for bats because they provided a large pool of older and mature trees in a variety of decay classes as roost sites. With short logging rotations in the jarrah forests and with only approximately 39 % total forest area currently reserved from logging in the study area, the roosting requirements of bats may be affected negatively as the abundance of old trees with hollows, exfoliating bark and other forms of senescence may be reduced. Thus, although this study demonstrated the importance of mature forest and buffers as mitigating measures on bat roost sites, it was unclear whether the area of retained habitat is adequate for for roosting bats given the dynamics of logging regimes in the jarrah forests, and this should be a priority to address in future research.

As the only mammals capable of true flight, bats may persist in selectively logged forests. However, as this study showed, bats are specialised in their foraging and roosting requirements. Therefore, the maintenance of forest tracks and the protection, and sustained recruitment, of hollow-bearing trees are essential for the conservation of these animals in such modified landscapes. Current management practices in the jarrah forests have created a mosaic of successional stages within logged landscapes that may satisfy the foraging requirements of many bat species. This is especially true because tracks and unlogged buffers and structurally mature forest with reduced clutter provided access to post-disturbance forests such as regrowth areas. The study also demonstrated that habitat retention, as provided by adjacent streamside buffers and mature forest in the jarrah forests were important roost sites for bats, and could mitigate against logging impacts in the long term. However, retained habitat trees in

logged coupes were avoided by roosting bats and further studies are required to demonstrate if these can be used effectively by viable bat populations, especially in the absence mature unlogged forest and unlogged riparian buffers nearby. In addition, further research is required to shed light on bat overwintering and maternity roost sites that are important for the survival of bat populations. In addition, a long-term study to clarify temporal/seasonal and intra-specific variation in bat distribution and roost site selection needs to be undertaken in the jarrah forests of south-western Australia to better determine if current ESFM practices are effective at maintaining bat populations in logged forests.

Statement of Originality

I certify that the thesis entitled

Bat community structure and habitat use across logging regimes in jarrah eucalypt forests of South-western Australia

submitted for the degree of

Doctor of Philosophy

is the result of my own work and that where reference is made to the work of others, due acknowledgment is given.

I also certify that any material in the thesis which has been accepted for a degree by any other university or institution is identified in the text and duly acknowledged.

Tuesday, March 15, 2011

Paul W. Webala

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Preface

During my PhD project, I designed the study in collaboration with my supervisors, Michael Craig, Stuart Bradley, Bradley Law (informally), Kyle Armstrong, and Adrian Wayne. With the help of volunteers, I collected all the data; undertook all statistical analyses with assistance of my supervisors; drafted and revised all chapters (including those accepted for publications and/or already published); and took all photographs included in this thesis, with the exception of a few, which have been acknowledged.

Structure of the thesis

The main chapters in this thesis have been published as journal articles and are indicated below:

Chapter 3: Webala, P. W., Craig, M.D., Law, B.S., Armstrong, K.N., Wayne, A.F. & Bradley, J.S. (*in press*) Bat habitat use in logged jarrah eucalypt forests**,** south-western Australia. *Journal of Applied Ecology*, no. doi: 10.1111/j.1365-2664.2010.01934.x

Chapter 4: Webala, P. W., Craig, M.D., Law, B.S., Wayne, A.F. & Bradley, J.S. (2010) Roost site selection by southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi* in logged jarrah forests; south-western Australia. *Forest Ecology and Management* **260**, 1780–1790.

The articles were written with the support of some or all of my supervisors, who have therefore been included as co-authors (indicated below).

Names, addresses and roles of supervisors and/or co-authors (in alphabetical order)

- **Adrian F**. **Wayne**, Science Division, Department of Environment and Conservation, Locked Bag 2, Manjimup, WA 6258, Australia. Overall supervision of thesis, especially with regard to fieldwork and assisted with the drafting and editing of Chapter 4 and the subsequent drafting of the manuscript arising thereof for publication
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Chapter 1

General Introduction

In the recent decades, there has been a growing recognition of bats (Order Chiroptera) as important members of ecosystems, both due to many important roles they perform (e.g. insect control, seed dispersal, plant pollination, etc.) and their sensitivity to disturbances (Kunz and Lumsden, 2003; Fukui *et al*., 2006). As a consequence, there has been an increased concern for the conservation status of many species of forest bats (Pierson, 1998), but their small size, nocturnal habits and high mobility make bats a difficult group to study, and there are numerous gaps in their basic biology, habitat ecology and response to human disturbances (Fenton, 1997). The consequence of this is that even the most basic habitat associations of most species remain largely unknown. Forest bats are particularly poorly known, and targeted research is needed to reveal much about their habitat requirements and biology, which can be used to test and refine forest management practices (Law, 2004).

1.1 Impacts of logging on forest ecosystems, insects and bats

For decades, there has been an intermittent but raging debate on whether forests should be left intact for biodiversity conservation or managed to allow sustainable timber harvesting. However, owing to a growing demand for timber and other forest products, it has been proposed, albeit with caveats, that modified logging operations can proceed without compromising biodiversity conservation (Eyre and Smith, 1997; Lindenmayer and Franklin, 2002; Peters *et al*., 2006). Therefore, an understanding of the degree of species sensitivity and the plasticity of species' responses to different types of logging would be of great value in conservation and management planning. A key challenge for forest managers is the need to understand which components of

the fauna can persist in these logged habitats, which factors influence the maintenance of viable populations, and how forest dynamics can be effectively managed for both timber production and biodiversity conservation.

Continued research is required to assess the effectiveness of management practices and other forms of human-induced disturbances in forests, including on various faunal groups such as bats (Law, 1996; Law, 2004). Bats may be an ideal group to examine the effectiveness of management practices because they are an important component of mammalian diversity, play key roles in forest dynamics and may be good indicators of disturbance (Clarke *et al.*, 2005). Bats are, typically, good indicators of the integrity of ecological systems because individual species display a range of sizes, mobilities and longevities and fill a variety of trophic levels (Altringham, 1996; Kunz and Fenton, 2003). However, lack of information about habitat use by individual bat species means that the full potential of using bats as indicators of the conditions of a particular habitat, community, or ecosystem remains unclear (Fenton, 2003).

Various reviews show that forestry activities pose a significant threat to bat populations (Law, 1996; Richards and Hall, 1998), for instance, eleven species of Australian bats are threatened by forest harvesting (Duncan *et al.*, 1999). However, owing to the diverse forms of logging and other forms of forest disturbance worldwide, it is unrealistic to generalize the impacts of such disturbances across broad geographic regions (Lloyd *et al.*, 2006). Logging alters vegetation structure by modifying and simplifying forest structural and floristic complexity (Mueck and Peacock, 1992; Recher, 1996), disrupting ecosystem processes (Norton and Kirkpatrick, 1995), and fragmenting forest landscapes (Recher and Lim, 1990). It is, however, doubtful whether the level of fragmentation caused by logging has great impact on bats given their high mobility (Law *et al.*, 1999). This implies that logging affects bats primarily by altering forest structure and

floristics and disrupting ecosystem process, and the extent to which these changes affect forest function and composition (defined in table 1.1 below) is largely related to the intensity of harvesting practices.

Table 1.1. Definitions of forest structure, function and composition (from Lindenmayer and Franklin, 2002; Franklin *et al*., 2002)

Term	**Definition**
Forest structure	The presence of key structural attributes in stands (such as large diameter trees and logs, understorey thickets and canopy gaps) and the spatial arrangement of these attributes. Structure includes both the variety of individual structures, such as trees, snags, and logs of various sizes and conditions, and the spatial arrangement of these structures, such as whether they are uniformly spaced or clumped. It is a pattern in three dimensions, which can be described both horizontally and vertically. In the horizontal level, patterns of openings, closed forest, tree size and species are part of the structure. In the vertical level, the number of layers between the ground surface and the uppermost canopy are a key component of structure
Forest function	The ‘‘work’’ carried out by an ecosystem, including such processes as productivity, conservation of nutrients, and regulation of hydrological cycles.
Forest composition	The variety and abundance of species which present a major aspect of biodiversity

Timber harvesting leads to loss of features that are important roosting habitats for bats. One structural element of forest that is typically severely affected by logging is hollow-bearing trees. Recent studies have found that the number of trees with hollows that occur, and were perpetuated, on logged sites is negatively related to factors such as intensity of logging, the total number of trees retained after logging, the length of logging rotation, and the intensity of post-logging fire used to treat sites after harvesting, which themselves are inter-related (Gibbons and Lindenmayer, 2002). Currently in production forests, there is an increased protection of old-growth forests, and increased retention of unlogged buffer zones between logged areas and river and stream zones, to act as wildlife corridors, or as reservoirs for recruitment in harvested areas (CCWA, 2003). Old-growth is a forest which contains large, old trees and associated structural features such as large snags, large crown gaps and tree hollows and/or fallen trees (RAC, 1992). Old-growth forest is thus important, as these attributes are rare or absent in logged forests, and, together with retained buffer zones, this habitat is crucial for the persistence of forest-dependent bats in disturbed habitats such as logged forests.

Bats are either likely to rely on old growth forests or forests with old-growth attributes, such as hollows in large, old trees and associated arthropod food sources (Scotts, 1991; Recher, 1996; Parnaby and Hamilton-Smith, 2004). The importance of tree hollows as roosting and breeding structures for a large range of Australian wildlife, including many bats, has been the subject of substantial literature (e.g., Taylor and Savva, 1988; Hosken, 1996; Gibbons and Lindenmayer, 2002; Gibbons *et al*., 2002; Grove *et al*., 2002; Lindenmayer *et al.,* 2002; Kunz and Lumsden, 2003; Law, 2004). The presence, abundance and size of hollows are positively correlated with tree basal diameter, an index of age (Lindenmayer *et al.*, 1991; Bennett *et al*., 1994; Ross, 1999, Soderquist, 1993; Gibbons *et al.*, 2000), as tree hollow formation is a long process and a characteristic feature of tree senescence (Mackowski, 1984; Inions *et al.,* 1989). In production

forests, there is a general reduction in tree hollow availability as timber harvesting operations, including silvicultural management, lead to creation of large areas of younger aged forests. Hence, in such forests the number of hollow-bearing trees is typically reduced compared to unlogged forests. Therefore, where tree hollows are absent, or present in only low numbers such as logged forests, hollows become a critical limiting resource for hollow-dependent species (Russo *et al*., 2004).

Old growth forests are expected to contain more old trees with hollows than young regrowth forests because hollow formation is a long and complex process, often taking hundreds of years (Mackowski, 1984; Wormington, 1996; Gibbons *et al*., 2000). Hollow formation is associated with large tree diameter, tree height, advanced tree age, tree health and tree species (Gibbons and Lindenmayer, 2002). Therefore, larger and older trees are expected to have more and larger-sized hollows, having experienced longer periods of exposure to processes of cavity formation and development than smaller trees (Bennett *et al.,* 1994; Sedgeley and O'Donnell, 1999*b*). Some species of bats are reported to roost in tree crevices including cracks in tree trunks and in larger branches, and crevices created by bark rugosity. Perkins and Cross (1988) reported that silver-haired bats prefer roosting in old (> 150 years) Douglas-fir (*Pseudotsuga menziesii*) forests in Oregon, probably because of the bark characteristics of old trees. The bark of old trees tends to provide more crevices by separating more widely from the trunk (Russo *et al*., 2010). Old trees also develop more pronounced ridges and crevices in the bark itself. Furthermore, the formation of a well-developed understorey and the whole structural complexity of vegetation can also take hundreds of years (Mueck *et al.,* 1996), and the replacement of decayed logs on the forest floor can take even longer (Recher, 1996). The long recovery period after logging required for the critical old-growth resources to regenerate makes bats vulnerable, given the short logging rotations prevalent in Australia (Parnaby and Hamilton-Smith, 2004). Clearly, this has important

implications for the long-term conservation of insectivorous bats dependent on such resources. Therefore, it is crucial that management prescriptions retain sufficient old-growth elements after logging. However, whether bats use these retained old growth habitats, whether the habitat is sufficiently large to allow for temporal changes in food and roost requirements, and how much habitat is enough for the long-term persistence of bats has not been established (Law, 1996).

Apart from impacts on roosting requirements, logging also creates cluttered forests that differ greatly in structure from unlogged mature forest, and this influences how bats use these regrowth forests after logging. Emerging evidence indicate that the presence of flyways (forest tracks, riparian areas and small gaps) facilitate the use (foraging, commuting, drinking) of regrowth forest by many bats, which would otherwise avoid such cluttered habitats. For instance, although most studies report lower bat activity within regrowth forest than in recently logged or unlogged forest due to vegetation clutter (e.g., Law and Chidel, 2001, 2002), similar bat activity levels are reported on flyways between regrowth and old growth forests (Law and Chidel, 2002; Lloyd *et al*., 2006). However, with unambiguous evidence indicating that old forests are important roosting habitats for insectivorous bats (e.g. Lunney *et al*., 1988; Taylor and Savva 1988; Sedgeley and O'Donnell, 1999*b*; Law and Anderson, 2000, Law and Chidel, 2004; Rhodes and Wardell-Johnson, 2006), bats may persist in regrowth forest after logging as long as there are sufficient flyways, but will most likely roost in old-growth forests if these are available adjacent to selectively logged forests (Lloyd *et al*., 2006). Thus, the provision and maintenance of flyways in regrowth forests that would allow use by many foraging and commuting bats, which would otherwise avoid such areas, may ameliorate some of the negative impacts of logging on foraging (Law and Chidel, 2002; Lloyd *et al*., 2006).

As discussed above, logging can have both direct and indirect impacts on bats. Direct impacts include the mortality of bats during logging, while indirect impacts include the removal of large trees with hollows required by many roosting bats and changes to forest structure leading to denser, more cluttered regrowth forest inaccessible to many foraging bats. An additional indirect impact is through changes in prey availability. These changes in prey availability can result from changes in prey abundance, such as a reduction in abundance of many insect groups, such as moths and beetles, which depend on dead wood and large trees as habitat (Lawton *et al*., 1998; Forkner *et al*., 2006; Müller *et al*., 2007; Summerville and Crist, 2008), Alternatively, changes in prey availability may occur when the abundance of insect food species are not impacted by logging but become inaccessible to bats in the dense, cluttered regenerating regrowth forest where prey is abundant (Law & Chidel 2001, 2002; Adams *et al*., 2009).

1.2 Bat responses to logging impacts

Bats have a high tolerance of landscape modification owing to their ability to fly and the ease with which they can cross open areas (Kalko *et al*., 1999; Medellín *et al*., 2000; Rhodes and Wardell-Johnson, 2006). Different species of insectivorous bats respond differently to logging, and resulting changes in vegetation structure (Law, 1996; Brigham *et al*., 1997b; Law and Chidel, 2001, 2002; Patriquin and Barclay, 2003), depending on morphology, mobility and plasticity in foraging behaviour and diet (Bullen and McKenzie, 2001; Clark *et al*., 2005). It is, therefore, possible to predict the responses of bats to the effects of logging on the basis of their echolocation call attributes, wing morphology, flight performance and foraging strategy (Aldridge and Rautenbach, 1987; Fenton, 1990; Law, 1996; McKenzie and Muir, 2000).

There is generally lower bat activity for all species in thick, cluttered regrowth, compared with more open unlogged forest (Law and Chidel, 2002). Species with small home ranges and special

diets and/or roosting requirements, such as forest gleaners, may be especially susceptible to forest disturbance (Clark *et al*., 2005). This is, however, probably true only for periods immediately after logging. For instance, *Nyctophilus gouldi*, which has a low aspect wing ratio that allows slow flight and high manoeuvrability, was found to have similar activity levels in cluttered (16 and 22 year old) regrowth and more open unlogged forest (Law and Chidel, 2001, 2002). At the species level, therefore, bat activity in cluttered regrowth areas appears to vary, depending on whether each individual species is clutter-sensitive or clutter-tolerant (defined and discussed below). Law and Chidel (2002) found that both clutter sensitive and clutter-tolerant species had high activity on tracks when surrounded by regrowth but activity of clutter-sensitive species was negatively related to regrowth and rainforest clutter when sampled off-tracks.

Aside from tracks, riparian zones have recently been reported to be important habitats for bats in timber production forests. Current forest harvesting practices require that riparian buffers are not logged to ameliorate impacts to riparian areas (CCWA, 2003). The goals for such buffers include reduction of soil erosion, and the protection and restoration of habitat for wildlife. Riparian zones provide foraging and drinking habitat (Law and Chidel, 2002), as well as roosting habitats for many bats (Lunney *et al*., 1988, Taylor and Savva, 1988; Law and Anderson, 2000; Schulz, 2000). The presence of tracks and riparian zones facilitates the use of regrowth forest by clutter-sensitive and some clutter-tolerant species (Law and Chidel, 2002; Lloyd *et al*., 2006). Lloyd *et al*. (2006) found that bat activity, foraging rates and species richness were similar in buffered streams surrounded by logged, regrowth and mature forests, suggesting that riparian areas effectively provide habitat for foraging and commuting bats in selectively logged forests.

The activity of bats in different habitats largely depends on their morphology, mobility and plasticity in foraging behaviour and diet (Bullen and McKenzie, 2001). This in turn has led to

the grouping of bats according to their ability, or inability, to forage in certain habitats. For instance, gleaners have been described as closed microhabitat bats (Fenton, 1990) or as narrow space gleaning foragers (Schnitzler *et al*., 2003, Russo *et al*., 2007), many of which may not use echolocation calls for detecting prey but rather listen for sounds generated by their prey (Faure *et al*., 1990). Passive listening is also used to avoid alerting prey (Siemers and Schnitzler, 2004). Schnitzler *et al*. (2003) suggest that these bats use echolocation, with a few exceptions, solely for spatial orientation. The background vegetation and other clutter in closed microhabitats provide background acoustic contamination or barriers to echolocation calls and may impede flight as well (Fullard *et al.*, 1991, Arlettaz *et al*., 2001). Therefore, instead of using echolocation to detect and classify prey and to localize its position, they listen for prey-generated cues, or use low-intensity echolocation calls that are short (<2 ms), faint (<70 dB sound pressure level), high in peak frequency (> 50 kHz) and generally broad-banded (Neuweiler, 1983; Fenton, 1990). Little forest bats, *Vespadelus vulturnus*, are a good example of bats that have clutter-tolerant echolocation calls and a highly manoeuvrable flight pattern (O'Neill and Taylor, 1986).

Non-gleaners that feed by slow hawking in vegetation have broad wings and low wing loadings, giving them excellent low speed manoeuvrability. These bats have been described as narrow space flutter-detecting foragers (Schnitzler and Kalko, 2001; Schnitzler *et al*., 2003). Narrow space flutter-detecting foragers emit signals comprising a long, constant frequency component followed by a frequency-modulated terminal sweep (CF-FM) and with the Doppler shift compensation and a specialized hearing system, these bats can recognize echoes from fluttering prey insects modulated in the rhythm of the beating wings between unmodulated background echoes (Schnitzler *et al*., 2003). In contrast, high flyers (i.e. above the canopy) with long thin wings such as Old World molossids, which forage in open habitats, are typically clutter sensitive because they are unable to negotiate cluttered habitats (Humes *et al*., 1999). These bats are less

manoeuvrable and unable to negotiate cluttered spaces within forests due to their flight morphology (Neuweiler, 1984; Aldridge and Rautenbach, 1987; Barclay, 1988). High flyers emit signals that are longer (> 10 ms), with lower frequencies (10-30 kHz) and are more intense (> 100 dB SPL) to allow long-distance resolution (Fenton, 1990). High flyers, with high aspect ratio wings and high wing loadings (Norberg and Rayner, 1987), typically use low frequency, narrowband shallow FM or constant-frequency (CF) search calls up to 60 ms in duration (Fenton, 1990; Schnitzler *et al*., 2003). In the absence of background targets, these bats, described also as open space foragers, use echolocation predominantly for prey acquisition (Schnitzler *et al*., 2003). For example, the white-striped freetail bat (*Tadarida australis*, Chiroptera: Molossidae) which is a fast-flying species and predominantly forages in open areas well above canopy height (Churchill, 2003), uses a CF search mode call with characteristic peak frequency ranging from 11 kHz to 13 kHz (McKenzie and Bullen, 2003).

Many bats vary in their foraging behaviour and forage in more than one habitat (Schnitzler and Kalko, 2001). However, while bats that forage in open areas find it almost impossible to forage in cluttered environments such as beneath the forest canopy, clutter-tolerant species such as gleaners can forage in open areas (Fenton, 1990), although with potentially high energetic costs. Gleaners and other "closed habitat" bats would encounter severe flight limitations (in terms of physical flight) foraging in open areas because of their short, broad wings (low wing loadings and aspect ratios). This would appear to explain why some studies have found increased bat foraging activity in narrow passage ways and linear edges such as tracks and riparian zones (Law and Chidel 2001, 2002), including forest trails, which allow use by both clutter sensitive and clutter tolerant species in comparison to low bat activity in cluttered habitats, which is mostly dominated by clutter-tolerant species.

It is possible to predict the responses of bats to the effects of logging on the basis of their echolocation call attributes, wing morphology, flight performance and foraging strategy (Aldridge and Rautenbach, 1987; Fenton, 1990; Law, 1996; McKenzie and Muir, 2000). On the basis of eco-morphology, I predict specific species responses to a number of variables. Nine species of bats occur in the south west of WA (Fullard *et al*., 1991; Churchill, 2008), and it is expected that each species, or species groups, will respond differently to structural changes in vegetation after logging (Table 1.2).

Exceptions to the stated responses to logging are, however, expected in regrowth. In the presence of tracks and forest trails surrounded by regrowth, many bat species are predicted to persist on tracks but the less manoeuvrable molossids are expected to be affected off-track (Law and Chidel, 2002). The tracks and other flyways facilitate use of regrowth forests for clutter sensitive species, including fast flyers (Law and Chidel, 2002). In the dense canopy, fast flyers may be absent but may nonetheless persist by flying over the top canopy.

In old growth forest, where the forest has largely thinned out and there are large gaps and open spaces within the forest, bat activity is expected to be high for most species because the tree density and open spaces may match with optimal foraging opportunities because it contains enough space for less manoeuvrable species and is dense enough for species that prefer a more cluttered environment such as *Nyctophilus* spp. (Lumsden and Bennett, 2005). Whereas mature forest is likely to provide the greatest diversity of foraging options, logged areas that have a mosaic of habitat patches with some trails and flyways are also expected to have high bat activity (Law and Chidel, 2002; Lloyd *et al*., 2006).

Overall, bats such as *Chalinolobus morio*, *Nyctophilus gouldi*, etc., that have moderate aspect ratio and wing loadings in combination with multipurpose echolocation design, are expected to exhibit the greatest flexibility in foraging microhabitats (Fullard *et al*., 1991). Thus, silvicultural methods after logging are expected to have different immediate effects on different species of bats in south west WA.

Table 1.2. The expected responses of Western Australian bats to the post-logging effects in jarrah forests, south-western Australia, predicted from the eco-morphology and echolocation call attributes.

		Responses to logging effects							
Species	**Ecomorphology type**	**Negative**				**Positive**			
		Immediately post-logging	Young regrowth	Old regrowth	Old growth forest	Immediately post-logging	Young regrowth	Old regrowth	Old growth forest
Chalinolobus gouldii	• Edge space aerial forager • Moderate aspect ratio wings and moderate wing loadings	unaffected	Absent in dense regrowth	unaffected	unaffected	may forage in logged gaps	Forage on edges	Enough paces available for foraging	Enough spaces available for foraging
C. morio	• Edge space aerial forager • Moderate aspect ratio wings and moderate wing loadings	unaffected	Absent in dense regrowth	unaffected	unaffected	may forage in logged gaps	Forages on edges	Enough spaces available for foraging	Enough spaces available for foraging
Falsistrellus mackenziei	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Mormopterus species 4	• open space forager (High flyer) • high aspect	unaffected	Avoid dense regrowth	unaffected	unaffected	Activity high	Fly above canopy	Unaffected	unaffected

	ratio wings and high wing loadings • Less manoeuvrable in flight								
Nyctophilus gouldi	• Narrow space flutter detecting forager • Moderate aspect ratio wings and moderate wing loadings	affected	Activity high	Activity high	Activity high	may forage in logged gaps	Forages on edges and in dense regrowth	Enough spaces available for foraging	Enough spaces available for foraging
Nyctophilus geoffroyi	• Narrow space gleaning foragers • Low aspect ratio wings and low wing loadings	Affected because it gleans leaf surfaces for arthropods	unaffected	unaffected	unaffected	May still forage in open areas	Activity high	Activity high	Activity high
N. major	• Narrow space gleaning foragers • Low aspect ratio wings and low wing loadings	Affected because it gleans leaf surfaces for arthropods	unaffected	unaffected	unaffected	May still forage in open areas	Activity high	Activity high	Activity high

Tadarida australis	• Obligate open space forager (high flyer) • High flyer • high aspect ratio wings and high wing loadings	unaffected	Avoid dense regrowth	unaffected	unaffected	Activity high	Fly above canopy	Unaffected	unaffected
Vespadelus regulus	• Narrow space gleaning foragers • Low aspect ratio wings and low wing loadings	Affected because it gleans leaf surfaces for arthropods	unaffected	unaffected	unaffected	May still forage in open areas	Activity high	Activity high	Activity high

***** a = immediately after logging; b = intermediate time span corresponding to denser regrowth; c = old regrowth approaching mature structure; d = old growth forest

1.3 Roost selection by bats

Many species of wildlife that inhabit wood production forests, especially those that use hollows in trees are most vulnerable to the impacts of timber harvesting (Scotts, 1991; Gibbons and Lindenmayer, 1996). This is because hollows suitable as faunal nesting and breeding sites may take hundreds of years to develop (e.g. Mackowski, 1984; Gibbons *et al*., 2000; Whitford, 2002). The type of logging operations and the interval between harvesting rotations have a negative impact in hollow formation because these processes may prevent or severely impair the recruitment of trees with hollows (Recher, 1996; Gibbons and Lindenmayer, 1996). The consequence is that a large number of obligate or facultative hollow-using species, including many bat species, will be negatively affected (Gibbons and Lindenmayer, 1996).

Because bats spend a large portion of their life in roosts, specific associations and dynamics in the use of roosts offer insights into the complexity of habitat and resource use by various species (Kunz, 1982; Lewis, 1995). The choices made by bats with respect to the type and location of roost sites have a strong influence on their survival and reproductive success (Brigham and Fenton, 1986; Vonhof and Gwilliam, 2007). Roosts protect bats against environmental extremes and predators (Kunz, 1982; Tidemann & Flavel, 1987) and can be used as maternity, bachelor, migrating, and hibernation sites (Kunz and Fenton, 2003). They can also facilitate complex social interactions including information transfer (Kunz, 1982; Willis and Brigham, 2004), minimize parasite load (Lewis, 1996), promote energy conservation and reduce predation risks (Vonhof and Barclay, 1996; Rydell *et al*., 1996; Kunz and Lumsden, 2003). Roosts also provide shelter during the day and the night. Night roosts are defined as resting places between foraging bouts and provide places to ingest food transported from nearby feeding areas (Kunz and Lumsden, 2003). Bats select specific roost

sites on the basis of such factors as morphology, flight and echolocation capabilities, proximity to other resources (food, water, hibernation sites), climatic factors, and roost availability (Kunz, 1982).

A wide variety of roosts are used by bats in both natural and human-made structures (Kunz, 1982; Kunz and Lumsden, 2003), but more than half of the approximately 1100 species of bats rely on roosts in vegetation (Kunz and Lumsden, 2003). The majority of these use structures associated with trees, typically hollows (e.g. Sedgeley and O'Donnell, 1999*a*), cavities formed under bark (Foster and Kurta, 1999; Russo *et al*., 2004), and foliage (Hutchinson and Lacki, 2000). Mature standing trees, including snags, are likely to have the most available cavities and, therefore, are very important for bat roosting (Hutson *et al*., 2001; Lumsden *et al.*, 2002a). Some roost in structures built made by other animals such as bird nests (Schulz, 2000) while others may modify leaves of plants to construct tents (Balasingh *et al*., 1995). Anthropogenic structures such as buildings, churches, tombs, bridges and mines are also used by some bats (Entwistle *et al.*, 1997), while others shelter in caves and rock crevices (Fleming, 1988, Churchill *et al.,* 1997). The world's largest aggregations of bats are found in caves in both temperate and tropical regions, where millions of bats may be found in a single site (Hutson *et al*., 2001). Roosts in caves, mines and some rock crevices offer advantages of relative permanency, thermal stability and protection from climatic extremes (Kunz and Lumsden, 2003), but disadvantages in that they are patchily distributed. On the other hand, bat roosts under exfoliating bark and foliage are less permanent and vulnerable to environmental extremes but are more abundant and ubiquitous (Kunz, 1982).

Bats roost in foliage most frequently in tropical rainforests. Potential foliage roost sites are more abundant than cavity and crevice roosts, but their greater exposure makes them more

hazardous. Their abundance, however, makes them easy to find near foraging areas, and might help to reduce commuting distance (Kunz and Lumsden, 2003). The abundance of foliage roosts also facilitates the wide distribution of some foliage roosting species in the tropics. Foliage roosting bats also change roosts frequently in response to the transient nature of their roost sites. However, within the same season, they may show some fidelity to a general area (Kunz, 1982). These bats can roost high in the canopy, in subcanopy trees, or in understorey foliage and roost sites may be in dense foliage, in relatively exposed locations, among leaves, or on branches. For instance, the bat *Murina florium* roosts in vertically suspended clusters of dead leaves in the rainforest understorey in northern Australia (Schulz and Hannah, 1998). Sites may be concealed from above, but conspicuous from below (Kunz, 1982), an arrangement that presumably reduces their visibility and accessibility to predators, but permits them to take flight readily.

Many temperate insectivorous bats, especially in the family Vespertilionidae, use tree hollows as roosts (Sedgeley and O'Donnell, 1999*b*; Kunz and Lumsden, 2003). Tree hollows generally provide a relatively stable microclimate that differs from the external ambient microclimate. Microclimate of a cavity can be affected by aspect, entrance height, canopy cover, density of surrounding vegetation, tree status (alive or dead), thickness and insulating properties of the cavity walls, tree diameter, cavity size, and number of bats occupying the cavity (Kunz and Lumsden, 2003). Sedgeley (2001) reports that cavities used as maternity roosts by *Chalinolobus tuberculatus* are insulated against temperature extremes and have significantly smaller temperature and humidity ranges relative to external ambient conditions. A warm, thermally stable environment for female bats minimises the energetic cost of thermoregulation and this improves their reproductive success (Racey, 1973).

Bats show intra-specific and seasonal differences in the location of roosts, with the most crucial sexual difference being in the choice of maternity roosts. For instance, Australian bat species of both sexes such as *Nyctophilus bifax* (Lunney *et al.*, 1995), *N. geoffroyi* (Taylor and Savva, 1988; Lumsden *et al.*, 2002*b*), *N. gouldii* (Lunney *et al*., 1988; Tidemann and Flavel, 1987), and *N. timoriensis* (Churchill, 2008) may use spaces beneath exfoliating bark for roosting. However, while these bats roost under bark most of the year, maternity roosts of many of these species occur in tree hollows rather than under exfoliating bark (e.g., Lumsden *et al*., 20002*b*), highlighting the importance of tree hollows as key roosting resources for bats. A few exceptions are, however, reported in maternity colonies of European barbastrelle bats (Russo *et al*., 2004) and American Indiana bats (Timpone *et al*., 2010) , which select roosts beneath loost bark.

While maternity roosts are typically located in well-insulated tree cavities (Sedgeley, 2001; Lumsden *et al*., 2002b), male bats often roost singly in shallow tree cavities or under exfoliating bark (Law and Anderson, 2000; Kunz and Lumsden, 2003). The roosts of solitary males are thus expected to provide little thermal insulation against external fluctuations in ambient temperatures (Hosken, 1996; Lumsden *et al*., 2002b; Turbill *et al*., 2003*a, b*). Males compensate for the lack of insulation in their often exposed roosts by switching between torpor and normothermic thermoregulation and they appear to gain energetic advantages by doing so (Turbill, 2006). Reproductive female bats, in contrast, show reluctance to enter torpor in field conditions. Turbill and Geiser (2006) attribute the observed differences between the sexes to ecological rather than physiological differences, which reflect the fact that females roost gregariously, whereas male bats typically roost solitarily. Pregnant females roost together because they need homethermic conditions while males are daytime torpid to save energy. Generally, many Australian vespertilionid bats roost under highly variable

conditions during the day because they have evolved energy conserving physiological traits such as low basal metabolic rate and an ability to enter torpor (Willis *et al*., 2005).

Tree cavity choice by bats is affected by such factors as tree structure, age, size, and height, with most suitable cavities located in the oldest, largest and tallest trees. The age of cavity-bearing trees is important to bats to the extent that it is a factor in frequency of cavity formation, cavity size, and cavity characteristics (Tidemann and Flavel, 1987). Lunney *et al.* (1988) found that large diameter trees, of more than 80 cm diameter at breast height over bark (DBHOB)., are selected for roosting by Gould's long-eared bat (*Nyctophilus gouldi*), a cavity- and crevice-roosting species. Similarly, the eastern forest bat (*Vespadelus pumilus*) was found to predominantly select roosts in large diameter mature trees in two areas with different disturbance histories in northern New South Wales (Law and Anderson, 2000). Large diameter trees are, however, typically rare in disturbed or modified habitats such as logged forests because they are targeted during logging operations for their quality timber (Lindenmayer, 1999).

Different bat species usually have specific roost requirements and all bats are secondary cavity users and do not excavate or greatly modify their own cavities but have to use available ones (Kunz, 1982). It is essential, therefore, for these bats to select sites with appropriate qualities, and many species are highly selective in their choice of roost trees and cavities (Vonhof and Barclay, 1996; Sedgeley and O'Donnell, 1999*a*, *b*; Law and Anderson, 2000; Lumsden *et al.*, 2002*a*, *b*). In New Zealand, although the Long-tailed Bat *Chalinolobus tuberculatus* changes roosts almost daily among a large group of different roosts (O'Donnell and Sedgeley, 1999; Sedgeley and O'Donnell, 1999*a*), the species is highly selective in its choice of roost trees and roost cavities (Sedgeley and O'Donnell, 1999*a*, *b*). Therefore, with

specific requirements for roost sites such as the selection of large old hollow-bearing trees as roost sites, any form of habitat disturbance such as timber harvesting is likely to affect the persistence of bats in such modified habitats.

1.4 Fidelity of bats to roosts

Patterns of roost fidelity by bats have been reviewed (Kunz, 1982; Lewis, 1995). Generally, an inverse relationship has been described between roost abundance and roost fidelity on one hand, and a positive relationship between roost permanence and roost fidelity on the other. Therefore, species using more permanent, less abundant types of roosts are expected to show greater roost fidelity than those using more abundant, ephemeral roosts (Lewis, 1995). For example, bats that roost in foliage should exhibit lower fidelity relative to cavernicolous species (e.g., O'Donnell and Sedgeley, 1999). Conversely, cavity-roosting species would be expected to exhibit higher fidelity relative to foliage-roosting species. This explanation may be belied by the fact that some roost trees may be reused over several years while keeping an updated picture of the condition of the cavities (Willis and Brigham, 2004).

Many temperate tree-roosting bats are known to exhibit a low degree of roost fidelity (Taylor and Savva, 1988; Lunney *et al*., 1988; Lumsden *et al*., 1994; Lunney *et al*., 1995; Law and Anderson, 2000; Lumsden and Bennett, 2000; Willis and Brigham, 2004; Russo *et al*., 2005), but roosting trees are often in close proximity (Lunney *et al*., 1988; Lunney *et al*., 1995; Kosken, 1996; O'Donnell and Sedgeley, 1999; Law and Anderson, 2000; Lumsden *et al*., 2002*a*; Kunz and Lumsden, 2003), underscoring the importance of maintaining multiple roosts within a diverse range of hollow-bearing trees, even when these hollows are not being used during part of the year (Law and Anderson, 2000; Law, 2004). Roost switching probably occurs to reduce predation, decrease commuting costs to foraging areas, increase awareness

about alternate roosts and minimise parasite loads. It might also be a response to altered social or climatic conditions (Lewis, 1995) or may result from a continual search for roosts with the right microclimatic conditions (O'Donnell and Sedgeley, 1999; Sedgeley and O'Donnell, 1999*a*; Sedgeley, 2001; Kunz and Lumsden, 2003). Roost switching may also reflect the maintenance of long-term social relationships between individuals from a colony that is spread among a number of different trees on a given night, and could serve to increase the numbers of individuals with which bats maintain associations, a pattern of behaviour known as a fission-fusion social structure (Kerth and König, 1999; Willis and Brigham, 2004).

1.5 The problem statement

In Australia, it is a generally accepted principle that reserve systems may not retain the original biological diversity of ecosystems and, therefore, wildlife management has been integrated in logging policies (RAC, 1992). It is also acknowledged that State forests are multiple-use areas and so biodiversity conservation is a dual aim with timber extraction. Several attempts have thus been made by most State forestry agencies to mitigate adverse effects of logging on wildlife, including bats, but mitigation measures are as diverse as the Australian regions (see Recher, 1996). Common measures across States include the following; (1) logged areas should retain hollow-bearing trees, (2) reduction in the size of individual logging areas, (3) corridors of unlogged forest are commonly retained between cut areas, (4) restrictions on logging in stream zones, and (5) protection of key habitat features for threatened or sensitive species. Tests of the efficacy of these measures and other management prescriptions in ameliorating the effects of logging on biodiversity are still in their infancy and much more research is required. Some studies suggest, however, that buffered protection zones, such as riparian zones, are effective in mitigating the impacts of logging on bat fauna.

For instance, the golden-tipped bat (*Kerivoula papuensis*) was found to select riparian rainforest for roosting on the south coast of New South Wales (Law and Chidel, 2004), and, therefore, the retention and protection of such habitats in logged areas may provide key habitat to such bat species.

Jarrah forest is a dry sclerophyll eucalypt forest type, located in the south west of Western Australia, is dominated with jarrah (*Eucalyptus marginata* Donn. ex. Smith, 1802) and with marri (*Corymbia calophylla* K.D. Hill and L.A.S. Johnson). In the jarrah forest ecosystems, about 2.4 million hectares of native forest are managed by the Department of Environment and Conservation (DEC) (Bradshaw *et al.*, 1991; RAC, 1992), 40% of which have been set aside as conservation and nature reserves. The rest of the forest is classed as State forest that is managed for multiple uses such as mining, timber production, recreation, wildlife conservation and water supplies (RAC, 1992; CALM, 1993). The former two are of great economic importance to Western Australia (CALM, 1987a; CALM, 1987b; CALM, 1987c) but, incidentally, have the greatest potential of causing deleterious impacts to the forest ecosystems if not well practiced. For instance, the northern part of jarrah forests has been leased for mining and thousands of hectares of forest have been cleared as a consequence (Bradshaw, 1999). The rest of the State forest is available for timber production, and almost all of the Jarrah forest has already been harvested for timber at some time in the past (CALM, 2001).

Past extensive clearing of jarrah forests raises the unequivocal question of whether multiple uses of the forests, and timber production and mining in particular, are compatible with the conservation of biological diversity. However, the current management practices (encompassing the retention of many landscape features such as riparian buffers, targeted

habitat for threatened species, etc.), albeit untested on a large scale, are expected to maintain forest structural diversity as well as retain multiple large, old trees in an area. It is hoped that the resulting logged landscape is sufficiently extensive to allow for temporal changes in roost and food requirements for bats and will help ensure their long-term persistence (Law, 2004).

While logging has continued in the jarrah forests for over a century, there were few baseline studies on the impacts of changes in forest structure and species composition as a result of logging on forest animal species prior to the 1990s (McKenzie *et al.*, 1996), although some studies are available on birds (Abbott and Van Heurck, 1985; Norwood *et al.*, 1995). In the neighbouring karri *Eucalyptus diversicolor* forest in Western Australia, bird species richness of regrowth takes 30–50 years to reach that of old-growth (Williams *et al*., 2001), but how long this takes in the jarrah forest is unclear. In the absence of baseline data, subsequent studies on assessing logging impacts were very controversial (Calver and Wardell-Johnson, 2004), with some studies suggesting that impacts were negligible (Abbot and Christensen, 1996), while others took the middle ground by stating that data were inadequate (Calver *et al.*, 1998) and the rest suggesting that adverse impacts were already occurring (Mawson and Long, 1994). However, recent population studies indicate population changes of some animal species after logging (Rhind, 1998; Craig & Roberts 2005) and fauna using tree hollows for shelter are expected to be particularly vulnerable to intense selective removal of large, old trees (Mawson and Long, 1994; Saunders and Ingram, 1995). McKenzie *et al.* (1996) report that some animal groups in south-west Western Australia forests have declined less markedly than those of other areas of the State, but with a caveat that changing land-use patterns is of great concern.

Some studies suggest that logging and related activities may not solely be threatening fauna in the jarrah State forests, but may actually exacerbate declines caused by more significant threats, such as forest clearance for agriculture and effects of introduced predators and plant pathogens (McKenzie *et al.*, 1996; Calver and Dell, 1998b; Calver and Wardell-Johnson, 2004). However, impacts of the changed vegetation structure due to timber harvesting on different faunal components vis-à-vis other threatening processes such as changed fire regimes require rigorous investigations (Calver and Wardell-Johnson, 2004).

In the new policy document *Protecting our old-growth forests*, there is a clear change of approach to the management of the State's jarrah and karri forests, and these include commitments to end logging of old-growth forests, establish a large number of new parks and reserves, and manage the State's forests in accordance with the principles of Ecologically Sustainable Forest Management (ESFM) (CCWA, 2004). The current Forest Management Plan (FMP) thus espouses principles of ESFM, and hopes to ensure biodiversity conservation, sustain the health, vitality and productive capacity of ecosystems and ensure that the social, cultural and economic benefits are valued by the community (CCWA, 2004).

Consequently, the FMP proposes certain actions that seek to conserve self-sustaining populations of native species and communities, at both local and landscape levels, and their recovery between timber rotations. These actions include the identification, protection and maintenance of a comprehensive, adequate and representative (CAR) reserve system and forest conservation areas that are not available for timber harvesting. The second vital element is the requirement for management practices in production forests to be sympathetic to biodiversity conservation. But in order to achieve the overall objectives for the maintenance of biodiversity, the forest is managed to minimize the adverse impacts resulting from resource

extraction, particularly timber harvesting. This means, for example, that there are areas within production forests (e.g. temporary exclusion areas, fauna habitat zones and informal reserves) that are not logged in the short, medium or long-term and should provide for the protection of many forest values (CCWA, 2004).

A supplementary component of the FMP is the retention of habitat elements in harvesting operations. Of critical importance, however, is the retention of old-growth forests, buffer zones between logged areas and river and stream zones free from timber harvesting to act as wildlife corridors or as reservoirs for recruitment into harvested areas. With proposed additions to the formal reserve system provided for in the FMP, over 90% of old-growth forest is protected in such reserves.

Still, in spite of the raft of management prescriptions implemented by the DEC and Forest Products Commission in the current FMP, any form of disturbance that leads to environmental changes will ultimately affect faunal populations. Moreover, whether the ESFM prescriptions are sufficient for the protection of flora and fauna is still a matter of conjecture as they remain largely untested (Calver *et al*., 1995, 1998). A study of insectivorous bats may be used to understand the ecological processes at work in the aftermath of logging, and amid ongoing changes resulting from years of logging because they are an important part of mammalian diversity. Bats anecdotally make up a significant proportion of the mammal fauna in the jarrah forest (9 of around 30 native extant species), but knowledge of them is relatively basic. Although some research has been undertaken into their response to logging and other disturbances in forested areas elsewhere in Australia (e.g. Law *et al.*, 1999; Law and Anderson, 2000; Law and Chidel, 2002; Lloyd *et al.*, 2006), to date there has been no comprehensive study of bat responses to logging in the south-west.

The project investigated impacts of logging on insectivorous bats at the individual species levels. As logging modifies vegetation structure, which in turn affects the foraging and mobility of bats (Humes *et al*., 1999; Law and Chidel, 2001, 2002), bat activity (foraging, commuting) was investigated in three forest types, namely, recently logged forest or gaps (<6 years since logging), young regrowth forest (12–30 years since logging) and old regrowth forest (> 30 years old) to test the hypothesis that logging reduces the abundance of the bats, particularly more specialised species. The abundance of nocturnal volant insects in the three forest types was also investigated contemporaneously with bat activity, as reductions in flying insect prey abundance are also known to occur due to logging (Law, 1996; Burford *et al*., 1999; Whitaker *et al*., 2000).

By examining the relationships between bat species assemblages and various variables that define the structure of vegetation on the one hand, and the relationship between bats and insect biomass on the other, the study sought to identify the effects of recent logging in the area on the bat fauna. In addition, whereas a number of studies have investigated the use of roosts by bats, especially in Eastern Australia (e.g. Taylor and Savva, 1988; Lunney *et al.*, 1988, 1995), knowledge of species' requirements for hollow-bearing trees still remains cursory in the eucalypt-dominated vegetation of Australia. Furthermore, temporal and spatial changes in the use of hollows by particular species, or by a range of taxa (intra- and inter-specific use of hollows), have yet to be examined. To find habitat trees, radio-collared bats were tracked back to their roosts (White and Garrot, 1990), allowing the location and identification of habitat trees. In Western Australia, little was hitherto known about roosting requirements of bats and the extent to which results from elsewhere in Australia can be extrapolated to Western Australia was not known. Therefore, using radiotelemetry, this study

assessed the roosting habitat requirements of two sympatric species of forest-dwelling bats, namely the southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi*. In turn, this information will help evaluate the sensitivity of these species to logging and whether ESFM management practices are effective in conserving populations of these species. The two species were selected because they have small home ranges and are fairly common, permitting easier tracking of the bats to their day roosts than would have been possible with wide-ranging and/or rare species (Marzluff and Sallabanks, 1998). Besides, the two species display different wing morphologies and echolocation call attributes, both potentially influencing how each species uses a logged landscape. The roost trees used by each species were compared to a random sample of available trees to test whether roost trees were distinct from the general population of available trees. Direct inter-specific comparisons of roost tree characteristics were made to determine whether each species exhibited preferences for particular tree and site characteristics.

The main aim of this study was to investigate effects of logging on the foraging, commuting and roosting requirements of bats in the jarrah forest, south-western Australia. Based on previous studies, I predicted that the nine extant bat species in the jarrah forests would respond differently to logging impacts according to their eco-morphology and echolocation call attributes. Specifically, clutter tolerant species with moderate wing loadings and aspect ratios were predicted to be ubiquitous in regrowth areas and other logging histories. Furthermore, roost trees of the two selected bat species were predicted to be larger and less cluttered by surrounding vegetation than random trees. Overall, the study hoped to test the hypothesis that, at the compartment level, logging alters the forest structure, which alters the roosting sites and foraging patterns of bats, and this may affect their long-term persistence. Specifically, the following predictions were tested;

- At the species level, different species were expected to respond differently according to their ecomorphology and echolocation call attributes (see section 1.4)
- Bat activity levels, are positively correlated with availability of insect prey, when measured as dominant dietary types
- Hollow-roosting bats will only use roosts in riparian buffers, contemporarily unlogged buffers zones and mature forest because these areas contain higher densities of hollow-bearing trees than recently logged forest.

1.6 Content of the thesis

This thesis consists of five chapters. **Chapter 2** introduces the study species, the study area and the logging history of jarrah eucalypt forests. **Chapters 3 and 4** include results of fieldwork undertaken in the jarrah forests, south-western Australia. **Chapter 5** concludes with an overall discussion of the main findings of the study and their management implications.

Chapter 3 describes the activity of jarrah forest bats at individual species level– including foraging patterns – along a gradient of logging histories (recently logged, young regrowth and old regrowth). The chapter uses information from bat call recordings using bat detectors, and light traps to sample invertebrate prey abundance, to answer the following questions: (1) What was the relationship between logging history and (a) bat activity, (b) bat foraging activity and (c) bat prey abundance; and (2) what was the importance of tracks and roads as commuting and foraging habitats of bats?

Chapter 4 investigates impacts of jarrah forest logging on the other key resource for bats – roosting resources. It uses information from telemetry of foraging bats to answer the following questions: (1) what distinguished roost trees used by two sympatric species of

jarrah forest-dwelling vespertilionid bats, the Southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi* from random trees at local and landscape scales?; (2) what were the similarities and differences between the two species in the choice of roosts at both local and landscape scales as influenced by logging impacts?; and (3) what was the relative importance of buffer zones and other unlogged zones as roosting habitat for bats in selectively logged jarrah forests, south-western Australia? This information is important to understand roosting patterns of bats, as roosting resources are likely to be limited in logged forests. Therefore, this information can be used to formulate management recommendations for the protection and retention of habitat trees and unlogged buffers in selectively logged jarrah forests in south-western Australia.

Chapter 5 summarises the key results and puts them into context, especially for the long-term persistence of bats in forests managed for both timber extraction and biodiversity conservation following the principles of ecologically sustainable forest management (ESFM).

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Chapter 2

Study species, study area and logging history

Plate 2.1. The chocolate-wattled bat (*Chalinolobus morio*).

2.1 Introduction

The overall goal of my thesis was to investigate possible post-logging impacts on the foraging and roosting ecology of bats. Nine bat species occur in south-western Australia and I investigated their activity in a range of forest types, as well as the roosting requirements of two selected species, *Vespadelus regulus* and *Nyctophilus gouldi*. This chapter provides a review of the study species, the study area and its climatic conditions and logging history.

2.2 Study species

A detailed description of the fauna of jarrah forests, south-western Australia can be found in Nichols and Muir (1989). General roosting and foraging aspects of the nine bat species that occur in the south-western Australia are described briefly below.

- Gould's wattled bat *Chalinolobus gouldii* (Gray, 1841). Most widespread species of small bat in Australia, found throughout Australia, Tasmania and Norfolk Island. The species has an average weight of 13.8g (10 – 20.0g) and forearm length of 43.7 mm (35.5-47.2 mm) in Victoria but the species is smaller in northern Australia (Churchill, 2008). Lumsden *et al*. (2002) found that *C. gouldii* has strong preference for live, large diameter trees relative to available artificial structures. In the same study, dead trees were used in proportion to their availability; including sprouts on outer branches that were particularly favoured. Elsewhere, *C. goudii* has been reported roosting in buildings especially in urban areas (Tidemann and Flavel, 1987), but the species prefers roosting in tree cavities if suitable trees are available (Lumsden *et al*., 2002).
- Chocolate wattled bat *Chalinolobus morio* (Gray, 1841). Endemic to Australia, this species occurs in Tasmania and widely across southern Australia, extending along the east

coast north to Townsville with several inland populations. *C. morio* has an average weight of 8.9 g (5.5 – 13.0g) and forearm length of 38.9 mm (33.0-42.4 mm (Churchill, 2008). Roosts mainly in hollows in old trees (Lunney *et al*., 1985), as well as disused birds' nests. They also roost in caves (Armstrong *et al*., 2005). They roost together in colonies of 20 to a few hundred bats.

- Western false pipistrelle *Falsistrellus mackenziei* (Kitchener, Caputi and Jones, 1986). Endemic to south-western Australia, the species is the largest vespertilionid in Western Australia. It has a mean weight of 21 g (17- 26 g) and a forearm length of 50.7 mm (48.0 – 53.7 mm). Its conservation status is Lower Risk (near threatened) (Duncan *et al*., 1999) and is listed by DEC as Priority 4. All available records are from the forested areas in mesic parts of the Darling Phytogeographic District of south-western Australia. Its range extends northward almost to Perth and eastward to the western margin of the wheatbelt. This bat is mainly restricted to areas of large trees, most particularly in the Karri, Tuart and higher rainfall areas of the jarrah forest. A specialist whose foraging niche centres on the 'inside stand /open' foraging microhabitat found under the canopy of mature forests (Duncan *et al*., 1999). The bat roosts in hollows, under loose bark or crevices of large trees (Churchill, 2008).
- Lesser long-eared bat *Nyctophilus geoffroyi* (Leach, 1821). Endemic in Australia, the species is widely distributed in mainland Australia, except the north east coast of Queensland, and also occurs in Tasmania (Churchill, 2008). It is a medium-sized bat, with a mean weight of 8.2 g (4.6- 14.5 g) and a forearm length of 37.1 mm (32.0 – 41.7 mm) in Victoria but it is smaller in northern Australia. *N. geoffroyi* roosts in hollows and fissures in old trees, under bark, in old Fairy Martin (*Petrochelidon ariel*) nests, and occasionally in caves. The species also sometimes roosts in ceilings, hollow walls, and canvas awnings in suburban and inner-city areas. In a study carried out in south-eastern Australia,

Lumsden *et al*. (2002) report that *N. geoffroyi* exhibits difference between sexes in the choice of roosts, and between breeding and non-breeding females. While males roosted in cracks and under bark of trees, fallen and decayed timber and artificial structures in low to high structures, females selected roosts higher above ground, and all were within trees. Maternity roosts were predominantly located in large dead trees, relative to non-breeding females, which roosted under bark and in cavities of smaller diameter trees. Cavities in large dead trees were therefore critical resources for *N. geoffroyi* because maternity roosts were only located there. Similar findings are reported by Taylor and Savva (1988) and Hosken (1996), where *N. geoffroyi* favoured dead trees in relation to their availability. Turbill and Geiser (2005) suggest that the observed reluctance by reproductive females of *N. geoffroyi* to enter torpor in the field is predominantly because of ecological, rather than physiological, differences, which reflect the fact that females roost gregariously whereas males typically roost solitarily.

- Gould's long-eared bat *Nyctophilus gouldi* (Tomes, 1858). Endemic to Australia, *N. gouldi* occurs in eastern Australia from north Queensland through New South Wales and into Victoria. The species is also found in south-western Australia (Churchill, 2008). Size is larger in the south than in the north. Mean weight is 12.3 g (9.0 – 16.5 g) and a forearm length of 44.0 mm (40.0 – 47.7 mm) in Victoria. Lunney *et al*. (1988) report that *N. gouldi* selected roosts only in trees in the unlogged gullies in logged forest on the South Coast of New South Wales and the bats showed strongest preference for those trees with a diameter greater than 80 cm. In the same study, *N. gouldi* changed roosts almost daily, but often showed strong fidelity to a cluster of trees within a single coupe.
- Western greater long-eared bat *Nyctophilus major* (Gray, 1844). *N. major* occurs in south-western Australia. It has a mean weight of 13.6 g (11.5 – 17.5 g) and a forearm length of

45.5 mm (43.2 – 48.4 mm). Prefers roosting in tree hollows, fissures in tree limbs and under bark, often in mature or dead *Eucalyptus* (Churchill, 2008).

- Southern forest bat *Vespadelus regulus* (Thomas, 1906). *V. regulus* is endemic to Australia and is distributed in Queensland, Victoria, southern and south-western Australia, as well as in Tasmania and Kangaroo Island. This species has an average weight of 5.2 g (3.6 – 7.0 g) and forearm length of 31.2 mm (28.0 – 34.4 mm (Churchill, 2008). Taylor and Savva (1988) report that, in south-eastern Tasmania, even when *V. regulus* foraged in regrowth, this species, along with three others (*Vespadelus darlingtoni, Chalinobolus morio, Nyctophilus geoffroyi*), roosted only in mature forest in hollows of large diameter trees.
- South-western free-tailed bat *Mormopterus* Species 4 (undecided) (Churchill, 2008). The taxonomy of *Mormopterus* (Molossidae) is poorly resolved in Australia and one of the species that occurs in the south-western Australia has not been formally named (Duncan *et al*., 1999).Therefore, this species was previously referred to as South-western free-tailed bat *Mormopterus* spp. (form spp. 4 (O), after Adams *et al*., (1988). Weight ranges from 6.8 to 13.0 g (mean = 9.0 g) and forearm length from 30.6 to 35.7 mm (mean =33.6 mm). These are tree cavity-roosting bats but may also roost in roof cavities and in lengths of water pipes.
- White-striped free-tailed bat *Tadarida australis* (Gray, 1838). Endemic to Australia, the species occurs primarily south of the Tropic of Capricorn, except Tasmania. Average weight is 37.6 g (30.5 – 47.5 g) and the mean forearm length is 60.6 mm (57.2 – 64.5 mm (Churchill, 2008). *T. australis* roosts in mature to over-mature eucalypts either singly, in small groups of around 20, or in maternity colonies of up to 300 individuals (Churchill, 2008; Rhodes and Wardell-Johnson, 2006). In their study at suburban subtropical Brisbane, Rhodes and Wardell-Johnson (2006) report that *T. australis* selected roosts in

trees with the most numbers of hollows in the trunk and branches. Additionally, chosen trunk cavities were large with large internal diameters. More importantly, *T. australis* roosted in highly urbanised areas and none of the roosts were found in neighbouring large forest reserves that apparently had suitable roosting trees and they attributed this to the fact that the species is generally suited to open habitats because of its flight morphology and echolocation call attributes.

2.2 Study area and logging history

The forested ecosystems of south-western Australia occur over an area of about 4.25 million hectares in three biogeographic regions namely Swan Coastal Plain, Jarrah Forest and Warren (IBRA bioregions *sensu* Thackway and Cresswell, 1995). The region has a Mediterranean-type climate with cool wet winters and warm dry summers (Dell and Havel, 1989). Annual average rainfall is about 700 – 1250 mm and its strongly seasonal nature is reflected in the ratio of winter (April to October) to summer (November to March) rainfall, which is about 6:1 (Gentilli, 1989). Jarrah forest is a dry sclerophyll forest type, with an overstorey consisting mainly of jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*), but with some yarri (*E. patens*) and bullich (*E. megacarpa*) in the gullies. The understorey is relatively sparse (Rhind, 2004) and includes species such as *Bossiaea aquifolium* and. *Lasiopetalum floribundum*, *Macrozamia riedlei*, *Xanthorrhoea gracilis* and *X. preissii* while midstory species include *Banksia grandis*, and *Persoonia longifolia*.

Major sources of disturbance arise from logging and associated practices such as road construction, prescribed fire, and other operations in State forests (Calver and Wardell-Johnson, 2004). Fragmentation of remaining native vegetation arising from extensive clearing for agriculture within and around State forests is also a conservation issue as well as clearing

for roads and powerlines and mining of bauxite, coal, tin and mineral sands (Wardell-Johnson *et al*., 2004).

Between the 1870s and 1920s, logging practices in many jarrah forests were uncontrolled but after that regulations were introduced and silvicultural practices have since evolved (e.g. Bradshaw, 1999; Calver and Wardell-Johnson, 2004; Wardell-Johnson and Calver, 2005; Stoneman *et al*., 2005). Less intensive, but more extensive, logging occurred between the 1940s and 1960s but from about 1970, logging reverted to intensive cutting aimed at reducing the area logged each year (Bradshaw, 1999; Stoneman *et al*., 2005). Since 1985, silvicultural practices resembling the group selection system of the 1920s have been introduced. In jarrah forests available for timber harvesting, one of three silvicultural systems will usually be applied to a patch of forest, depending on the existing stand structure and density of regeneration (Bradshaw 1999). These include the following:

(1) Thinning to promote growth on retained jarrah and marri trees;

(2) Removing the overstorey (creating gaps) to release and promote the growth of jarrah and marri advance growth existing as seedlings, ground coppice (advanced seedlings with well developed lignotubers) and small saplings. Maximum gap size is 10 ha, with most gaps being 4–7 ha;

(3) Cutting to retain a shelterwood to establish regeneration from seed where advance growth does not exist in sufficient density. Seedlings will be encouraged to establish and develop into ground coppice by reducing competition from the overstorey. A forest canopy is maintained (basal area about 13 m^2 ha^{-1}) to provide a continuity of forest values until the ground coppice is developed and capable of responding to release following canopy removal.

The choice of silvicultural treatment applied is determined following a ground survey of the extent and nature of existing regeneration. Habitat trees and habitat logs are identified and marked for retention, permanent buffers (unlogged areas) are retained along roads and streams and unlogged buffers are retained between coupes (coupe buffers). Coupe buffers may be logged in the next cutting cycle, some 15–30 years in the future. As a requirement, riparian areas are never available for timber harvest. In these cases, buffers extent for at least 20 m from the stream vegetation on both sides of the stream and is a minimum of 60 m wide (Craig and Roberts, 2005).

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Chapter 3

Bat habitat use in logged jarrah eucalypt forests of south-western Australia

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Subject to revisions

Plate 3.1. The Southern freetail bat (*Mormopterus* species 4).

Photo: Kellie Patterson / Paul Webala

Summary

1. Ecologically sustainable forest management is being implemented to address the competing demands of timber production and conservation, but its effectiveness is poorly understood. Bats play key roles in forest ecosystems and are sensitive to timber harvesting, so are potential indicators of whether management is successfully achieving biodiversity conservation in production forests.
2. We evaluated logging impacts in jarrah eucalypt forests of south-western Australia by examining insectivorous bat activity, feeding buzzes and insect biomass at four sites in each of recently logged forest, young regrowth and old regrowth.
3. Forest tracks supported higher overall activity and higher feeding activity than off-track sites, but activity was similar on-track irrespective of logging history. However, off-track activity in old regrowth was significantly higher than in either young regrowth or recently logged forest.
4. *Vespadelus regulus* and *Nyctophilus* spp. were more active in old regrowth than other logging histories. Similarly, *V. regulus*, *Nyctophilus* spp., *Chalinolobus gouldii*, *Chalinolobus morio* and *Falsistrellus mackenziei* activity was significantly greater on- than off-tracks, but activity was similar on-track across logging histories.
5. Increased understorey clutter was the strongest predictor of reduced bat activity in off-track sites. Reduced clutter and roost availability most probably explained greater activity in old regrowth forest. Neither insect biomass nor interactive effects of clutter and insect biomass significantly affected bat activity.
6. *Synthesis and applications*. Tracks provided internal linear edges within cluttered forests allowing bat species to use such areas for foraging. However, our results suggest that the retention of unlogged areas within logged forests is likely to be the

most effective strategy in many forest ecosystems for conserving bat populations and achieving ecologically sustainable forest management for this group.

Key-words: bat activity; eucalypt forest; clutter; logging; regrowth; track

3.1 Introduction

Forest logging is a major threat to global biodiversity (Sala *et al*. 2000) and a growing demand for timber means logging rates are increasing (Perry, Ram & Hart 2008). Consequently, there is a drive to develop forest timber harvesting strategies that maintain biodiversity alongside timber extraction. Attempts are therefore being made to integrate conservation into production forests according to ecologically sustainable forest management principles such as themaintenance of stand structural complexity and landscape connectivity and hetero-geneity (Lindenmayer&Franklin 2002).

Forest bats are one group with great potential for assessing the effectiveness of ecologically sustainable forestmanagement because they are typically sensitive to logging impacts and play key ecological roles in forest ecosystems, indirectly affecting other forest biota (Clarke, Rostant & Racey 2005). Although there are many ways in which logging affects forest bats (Hutson, Mickleburgh & Racey 2001), reductions in the quantity and suitability of foraging habitat, food resources or roosting sites are likely to be major impacts (e.g. Brigham *et al*. 1997; Forkner *et al*. 2006; Peters, Malcolm & Zimmerman 2006).

Reductions in the quantity and suitability of foraging habitat usually result from changes to forest structure post-logging. These changes can result directly from logging, through removal of large trees, or indirectly as logged forests regenerate with a different structure from

unlogged forest. Typically, logging regrowth is denser than unlogged forest, making it less suitable for many foraging bats, among other species (Law & Chidel 2001; Patriquin & Barclay 2003). Secondly, logged forests are usually traversed by flyways (tracks, including roads and trails), which allow bats to access and use forest that is otherwise too cluttered (Adams, Law &French 2009). Thirdly, logging can directly reduce food resources, such as moths and beetles, which depend on dead wood and large trees as habitat (Forkner *et al*. 2006; Summerville & Crist 2008). Lastly, logging can reduce the quantity and suitability of roosting sites. While forest bats roost in a variety of locations, the most severely affected are species requiring late successional features, such as peeling bark and tree hollows (Brigham *et al*. 1997; Law & Anderson 2000).

Jarrah eucalypt forests are dry sclerophyll forests restricted to south-western Australia that have been logged for over 100 years. Ecologically sustainable forest management was first introduced in 1985, with strategies designed to maintain biodiversity including selective logging, and retention of 12 habitat or potential habitat trees per hectare together with unlogged buffers within logged areas and around riparian zones (CCWA 2004). While logging effects on other fauna have been examined (e.g. Craig & Roberts 2005), it is unknown whether ecologically sustainable forest management is maintaining bat populations in production forests. Our study examined how jarrah forest logging affects bats through both changes in vegetation structure and prey populations. We hypothesized that the bat community does not differentiate forest habitats on the basis of forest age. However, at the species level, different species were expected to respond differently according to their ecomorphology and echolocation call attributes. For instance, we predicted that *Nyctophilus* species activity would be higher in forest away from tracks (off-track) than along forest tracks (on-track) given the species' low aspect ratio and wing loadings. Specifically, we tested the

hypothesis that logging history had no influence on bat activity, including foraging, and that bat activity was positively correlated with prey availability. Additionally, we hypothesized that tracks exhibited higher bat activity than off-track sites due to reduced vegetation clutter.

3.2 Materials and methods

STUDY SITE

The study area, located in south-western Australia (Fig. 3.1), has a Mediterranean climate. At the nearest weather station, temperatures in the coldest and hottest months average 9.6°C and 20.3°C, while annual rainfall is 1011.8 mm with > 70% falling between May and September (http://www.bom.gov.au/climate/averages/tables/cw_009573.shtml). Vegetation in the study area is jarrah forest, which has an overstorey dominated by jarrah (*Eucalyptus marginata* Donn. ex. Smith) and marri (*Corymbia calophylla* K.D. Hill and L.A.S. Johnson).

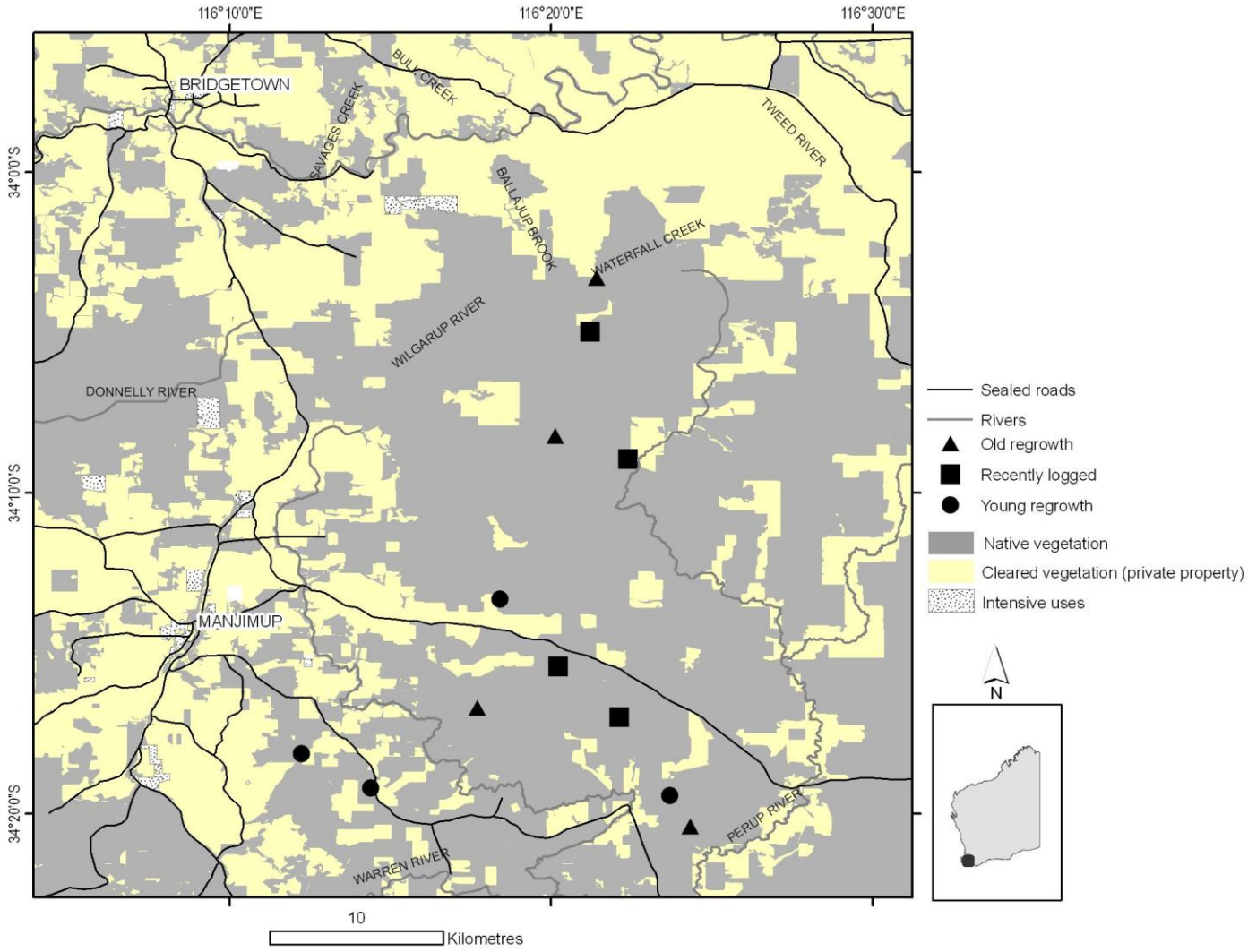

Fig. 3.1. Map showing the spatial arrangement of sampling sites. Inset shows the study area location within WesternAustralia

LOGGING HISTORY

Since new logging prescriptions were adopted in 1985, three types of forest can be identified: gap, shelterwood and buffer. Gaps involve removal of the overstorey to release and promote jarrah and marri growth from seedlings, ground coppice and small saplings. Maximum gap size is 10 ha and about 95% of tree basal area (the cross-sectional area of all trees 1.3 m above the ground) is removed with four habitat trees (those containing hollows suitable for fauna) and eight potential habitat trees retained per ha. By contrast, shelterwoods involve the retention of 40–60% of tree basal area to provide seed for regeneration. Finally, buffers are retained between gaps, around riparian areas and along major roads. These buffers are considered unlogged although they were probably lightly logged once after 1945.

EXPERIMENTAL DESIGN

We employed a two-factor orthogonal experimental design including three logging histories: recently logged forest (< 6 years post-logging), young regrowth (12–30 years post-logging) and old regrowth (>30 years post-logging); and two detector locations (on-track and off-track). Old regrowth contained forest attributes similar to unlogged forest, such as abundant hollow-bearing trees, but unlogged forest could not be included because< 5 ha of jarrah forest has never been logged (CCWA 2004).

Sampling was done at 12 sites that were previously logged, four sites for each logging history. Tracks are a universal feature of logged forests and consist of linear passageways ranging from 1 to 6 m wide and include forest trails and small roads that were unsealed (dirt or crushed stone). Bat activity and vegetation structure were assessed both on-track and off-track at each site, and insect abundance was sampled off-track only. We did not sample activity in riparian zones because they are not logged and so do not provide appropriate controls for

studying logging impacts (Law, Anderson & Chidel 1998). Bats typically travel 1–10 km per night (e.g. Lumsden, Bennett & Silins 2002), so sites were > 3 km apart to minimize pseudoreplication and interspersed with respect to logging history (Fig. 3.1).

BAT SAMPLING

Bat activity was recorded using Anabat SD1 Bat Detectors (Titley Electronics, Australia) 1 m above ground and oriented 40^{o} above horizontal to reduce sound attenuation by understorey vegetation. On-track detectors were set on the sides of, and parallel to, tracks, whereas off-track detectors were placed > 20 m from tracks and oriented away from them. To minimize bat call attenuation from vegetation at off-track sites, detectors were pointed towards small gaps (Law &Chidel 2002).

One site from each logging history was surveyed at both on- and off-track locations in November and December 2007 and 2008 (i.e. six detectors per night). Sampling was carried out during these months because bats breed at this time and so their resource requirements are highest. Each location was sampled for bat activity for two 2-night periods, totalling eight detector nights per site (four on-track and four off-track). All sites were sampled once before any sites were re-sampled. Sampling lasted from dusk to dawn with activity quantified as 'bat passes' (Fenton *et al*. 1998), defined as sequences of two or more distinct call pulses separated from the next set of pulses by >5 s (Law, Anderson & Chidel 1998). To compare habitat use, bat activity was indexed as the number of passes per night within each site/location. Additionally, feeding buzzes associated with prey attacks were identified and recorded as numbers of feeding buzzes per night at each site/location. To account for variations in bat activity due to temperature, we recorded minimum air temperature using

thermometers near off-track detectors. We did not sample on nights with rain or a full moon (Erkert 1982).

BAT CALL ANALYSIS

Calls were extracted using CFCread© software (C. Corben/Titley Electronics, Australia) and identified using Analook version 6 (C. Corben; http://www.hoarybat.com) by comparing call variables (e.g. frequency, pulse duration) with regional call libraries (e.g. Pennay, Law & Reinhold 2004). Due to geographic call variation, we collected reference calls from seven of the nine species known from the region and obtained recordings of the two remaining species from C. Corben (as above). Calls of three species, *Nyctophilus* major, *Nyctophilus gouldi* and *Nyctophilus geoffroyi* are indistinguishable (Pennay, Law &Reinhold 2004), so we lumped them as *Nyctophilus* spp.

INSECT ABUNDANCE ESTIMATES

We assessed insect prey availability using Australian Entomological Supplies funnel and bucket (diameter 26 cm) light traps with 12 V–8 W battery powered ultra violet lights (URL: http://www.entosuplies.com.au/). During the same months as bat activity, but on alternate nights to bat sampling to avoid confounding bat activity with increased insect activity around light traps (Adams, Law & French 2005), one light trap was placed on the ground in a clear open area (no vegetation cover) near off-track locations at all 12 sites from dusk to dawn for two different nights at each site. Minimum air temperatures were recorded near each trap.

Samples were sorted to order and wet biomass recorded. Dry biomass was estimated using the equation, Dry biomass = 0.0461*Wet biomass + 4.7024, derived from trials and subsamples. To obtain proxies for overall species abundance, given sorting and identification time

limitations, individuals of Lepidoptera and Coleoptera, were classified by size and specimens >1 cm body length identified to morphospecies.

VEGETATION STRUCTURE

We assessed vegetation clutter at all bat sampling locations in February and March 2008 using two10-m radius circular plots centred on bat sampling points. While vegetation sampling was done 3 months after bat sampling, the summer drought in these evergreen forests means that vegetation would have changed negligibly, if at all, since bat sampling. Within these plots, clutter (i.e. vegetation; Fenton 1990) in four strata [upper (≥ 15 m), midstorey (5–15 m), shrub (0.75 cm–5 m) and groundlayer stratum (0–0.75 cm)] was estimated as 1 (0–5%), 2 (5–25%), 3 (26–50%), 4 (51–75%) or 5 (≥ 75%) (Law & Chidel 2002). Because stratum height, and height differences between the two uppermost strata, can affect bat activity (Brown, Nelson & Cherry 1997), each stratum score was multiplied by its height to estimate clutter volume (Law & Chidel 2002). For instance, regrowth eucalypts often have extensive branching up their trunks, so multiplying that stratum cover by its height provides an index of clutter volume.

STATISTICAL ANALYSES

Prior to analyses, all data were transformed [ln (x + 1)] if they were not normally distributed or heteroscedastic. Nonparametric tests were applied when transformations were unsuccessful in rendering data normal and homeoscedasctic. All means are presented ± SE. Two-way multivariate anovas were used to test for differences in understorey and overstorey clutter indices between logging histories and track positions, with clutter indices as dependent variables. Differences between logging histories and track positions in overall and individual species bat activity, and feeding activity, were tested for both years using repeated measures

anovas with one within-factor (year) and two between-factors (logging history and detector position). *Post hoc* Tukey tests were performed to check for significant treatment differences (Day & Quinn 1989). Feeding buzzes were not analysed for five species because < 1% of passes by both *Tadarida australis* and *Mormopterus* species 4 were feeding buzzes, while *Nyctophilus* spp. may not use echolocation calls for detecting prey, but rather use passive listening (Grant 1991). Mormopterus is undergoing taxonomic revision, with Mormopterus species 4 representing an undescribed species equivalent to Mormopterus species 4 population 'O' in Adams *et al*. (1988).

Differences in insect biomass and abundance between logging histories and years were analysed using repeated measures anovas with one within-factor (year) and one between-factor (logging history). Only orders represented by >50 individuals were analysed individually. As insect activity was sampled at off-track locations only, insect abundance and biomass were compared with off-track bat activity only. To test if total dry insect biomass and insect abundance influenced bat activity, we conducted multiple regressions with total dry insect biomass and dry Lepidoptera biomass as independent variables, as these were the only insect variables that varied between logging histories, and overall or individual species bat activity as dependent variables. These data were analysed using Statistica 7.0 (Statsoft, Inc., USA). Where non-significant interactions were detected in repeated measures anovas, the models were repeated without non-significant interactions using mixed model analyses in spss 17.0 (SPSS, USA).

To analyse relationships between vegetation clutter and bat activity, we first examined correlations between clutter indices for each strata. Ground, shrub and midstorey indices were highly correlated ($0.82 < r < 0.86$, $P < 0.001$), but none were correlated with overstorey

clutter. Thus, in analyses, the three understorey indices were summed. Resulting understorey and overstorey clutter indices were then included in multiple regression analyses to test influences of vegetation clutter on bat activity, with individual bat species and overall bat activity as dependent variables. We used generalized estimating equations (spss 17.0) to determine the effects of vegetation clutter, insect biomass and their interaction on bat activity. Generalized estimating equations are extensions of Generalized Linear Models used to model correlated data, and they fit marginal models, where relationships between response and predictor variables are modelled separately from correlations between observations within each experimental or sampling unit (Diggle, Liang & Zeger 1994). For generalized estimating equations, each site or year was considered a cluster within which correlated data could occur and an independent correlation structure was used.

3.3 Results

VEGETATION CLUTTER

Both overstorey ($F_{2, 19}$ = 5.973; P = 0.010) and understorey ($F_{2, 19}$ = 10.392; P = 0.001) indices differed significantly between logging histories. Understorey indices did not differ between logged forest and young regrowth ($P > 0.05$), but both were higher than old regrowth ($P < 0.05$). Overstorey indices of all logging histories were different from each other ($P < 0.05$), with young regrowth the most cluttered and old regrowth the least (Fig. 3.2). Both understorey ($F_{1, 20}$ = 39.26; $P < 0.001$) and overstorey ($F_{1, 20}$ = 4.717; P = 0.045) indices were different between on-track and off-track locations, with more clutter off-track. Overstorey indices differed more at off-track than on-track locations, resulting in a significant logging history by detector position interaction ($F_{2, 19}$ = 0.80; P = 0.002).

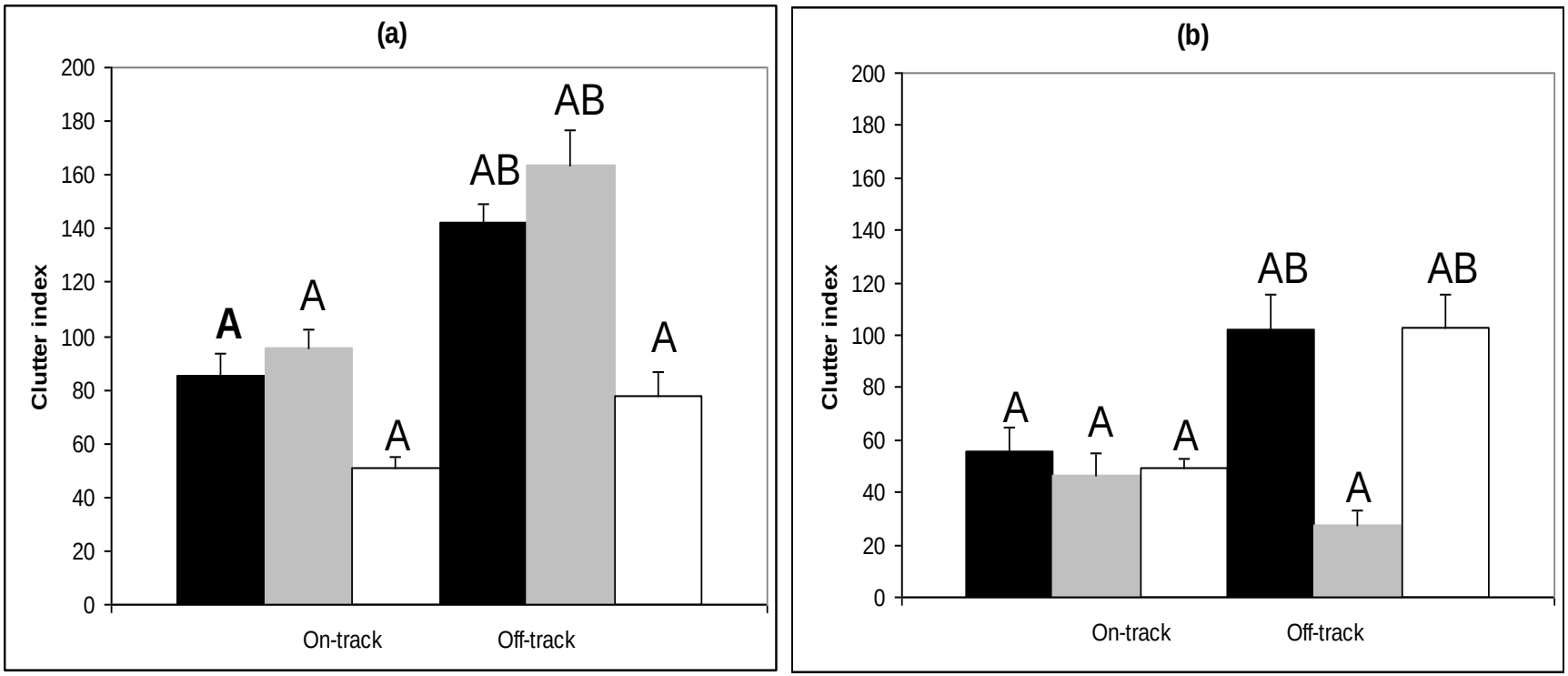

Fig. 3.2. Differences in vegetation clutter indices (untransformed mean ± SE) in three logging histories (young regrowth = black, logged forest = grey and old regrowth = white), on-track and off-track for (a) understorey and (b) overstorey. Different letters denote significant differences at $P < 0.05$.

BAT ACTIVITY RESPONSES TO LOGGING

We recorded 12 213 bat passes from nine species, 6110 in 2007 and 6103 in 2008, but 21% of recordings were unidentifiable and thus excluded. Of the remainder, 1.8% were unassignable to either *Chalinolobus gouldii* or *Mormopterus* species 4 and were included for total bat passes, but not for either species.

Although minimum air temperatures were lower ($F_{1, 42}$ = 27.23, P < 0.001) in 2008 than 2007, neither overall nor individual species bat activity was correlated with minimum air temperature (P > 0.05), so we interpreted logging impacts on bat activity independently of temperature.When data were pooled across years for both on- and off-track locations, old regrowth had more bat passes than young regrowth (P = 0.004) and logged forest (P = 0.012) with no difference between the last two logging histories (P = 0.957; Table 3.1; Fig. 3.3). There was also a significant logging history by year interaction due to logged forest recording more bat passes than young regrowth in 2007, but fewer in 2008. However, this does not change our interpretations of logging impacts because bat activity in both these logging histories was significantly lower than old regrowth in both years.

Differences in activity between logging histories only occurred off-track, with similar activity levels occurring on-tracks across logging histories (P > 0.05), resulting in a significant logging history by detector position interaction (Table 3.1). There was more activity off-track (P < 0.001) in old regrowth than either young regrowth or logged forest, which did not differ from each other (P = 0.996).

At the species level, logging history significantly influenced two species, *Vespadelus regulus* and *Nyctophilus* spp. *Vespadelus regulus* used old regrowth forest more (P < 0.01) than either

young regrowth or logged forest (Table 3.1). *Nyctophilus* spp. also used old regrowth more than either young regrowth ($P < 0.05$) or logged forest ($P < 0.01$), but there was a significant logging history by year interaction. In 2007, *Nyctophilus* spp. activity did not differ between logging histories, while in 2008 activity was higher in both young and old regrowth compared to logged forest.

Table 3.1. *F*-values from repeated measures ANOVAs for effects of logging history and detector position on bat activity, with year as within factor and logging history and detector position as between factors. Significant results are denoted by asterisks after models were rerun without non-significant interactions.

Species	**Logging history (LH)** ($F_{2, 34}$)	**Detector position (DP)** ($F_{1, 34}$)	**Year (Y)** ($F_{1, 34}$)	**LH x DP** ($F_{2, 34}$)	**LH x Y** ($F_{2, 34}$)	**DP x Y** ($F_{1, 34}$)	**LH x DP x Y** ($F_{2, 34}$)
Overall bat activity	14.54***	137.22***	0.002	8.09**	3.36**	-	-
Chalinolobus gouldii	0.17	15.43***	0.45	-	-	-	-
Chalinolobus morio	2.14	141.79***	0.00	-	-	-	-
Falsistrellus mackenziei	1.74	27.00***	0.22	-	-	-	-
Mormopterus species 4	0.20	0.46	0.46	-	-	-	-
Nyctophilus spp.	13.64***	28.67***	0.64	-	4.09*	-	-
Tadarida australis	1.06	0.11	11.72**	-	3.73*	-	-
Vespadelus regulus	15.34***	27.33***	0.08	-	-	-	-

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

FORAGING ACTIVITY RESPONSES TO LOGGING

We recorded 614 feeding buzzes (235 in 2007 and 379 in 2008) with *V. regulus*, *C. gouldii*, *F. mckenziei* and *C. morio* contributing over 99% of all feeding buzzes. Individual species feeding buzzes were not correlated with minimum air temperature ($P > 0.05$), so we assessed logging impacts on feeding buzzes independently of temperature.

Overall numbers of feeding buzzes differed significantly among logging histories (Fig. 3.4; Table 3.2) with more buzzes in old regrowth than either young regrowth ($P < 0.01$) or logged forest ($P < 0.05$) and no difference between the latter two ($P = 0.173$). *Vespadelus regulus* was the only species where feeding buzzes differed between logging histories, with more buzzes recorded in old regrowth and logged forest ($P > 0.05$) than young regrowth ($P < 0.01$) (Fig. 3.4; Table 3.2). Feeding buzzes also differed significantly between detector positions, with greatest foraging activity on-track (Fig. 3.4; Table 3.2) and all four species analysed showingmore feeding buzzes on-track (Fig. 3.4; Table 3.2). There were significant detector position by year interactions for *C. morio* and *F. mackenziei* as both species recorded significantly more feeding buzzes on-track in 2008 than 2007.

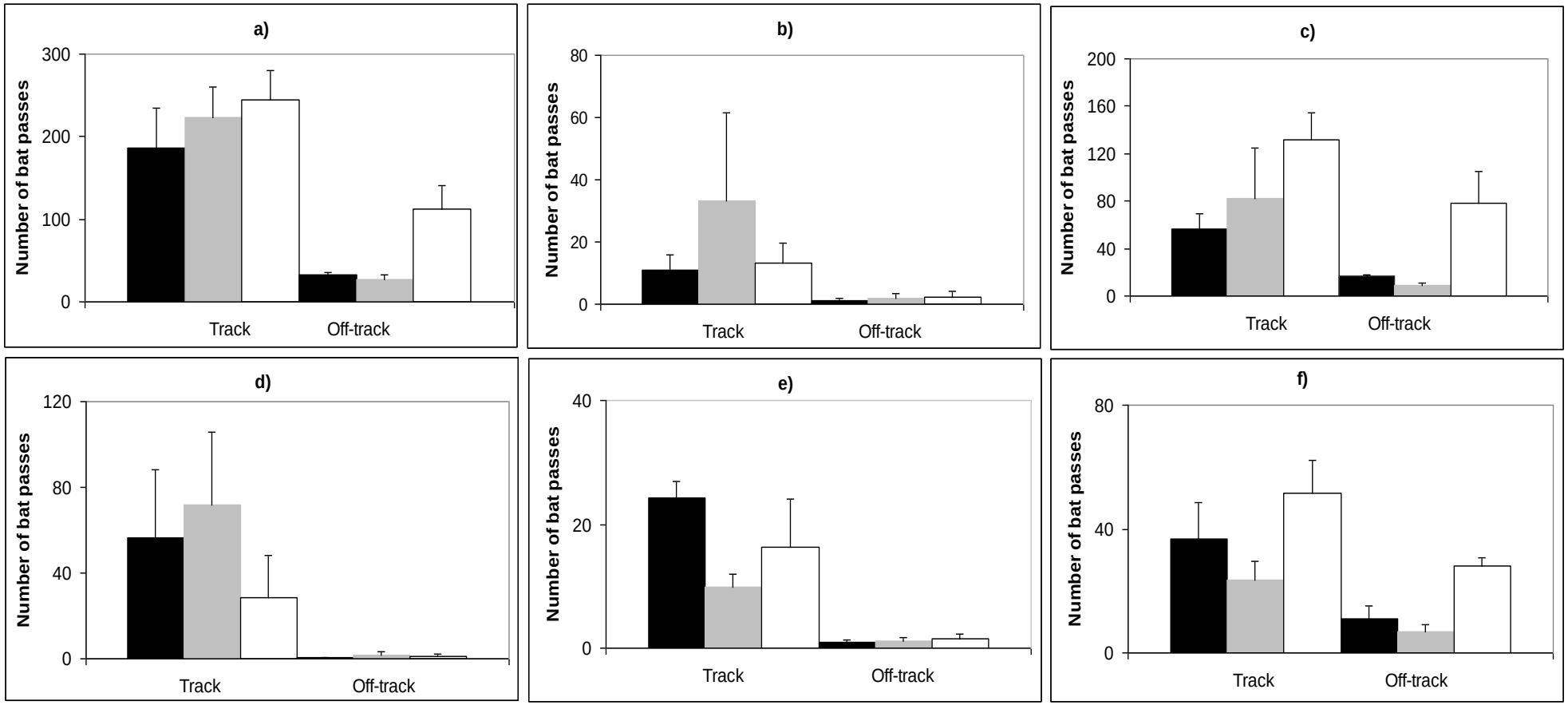
a)
Number of bat passes
300
200
100
0
Track
Off-track
b)
Number of bat passes
80
60
40
20
0
Track
Off-track
c)
Number of bat passes
200
160
120
80
40
0
Track
Off-track
d)
Number of bat passes
120
80
40
0
Track
Off-track
e)
Number of bat passes
40
20
0
Track
Off-track
f)
Number of bat passes
80
40
0
Track
Off-track

Fig. 3.3. Differences in bat activity (passes per night: untransformed mean ± SE) in three logging histories (same key as Fig. 3.2) in on-track and off-track positions for (a) overall bat activity, (b) *Chalinolobus gouldii*, (c) *Vespadelus regulus*, (d) *Falsistrellus mackenziei*, (e) *C. morio* and (f) *Nyctophilus* spp. Note that y-axis values vary between species.

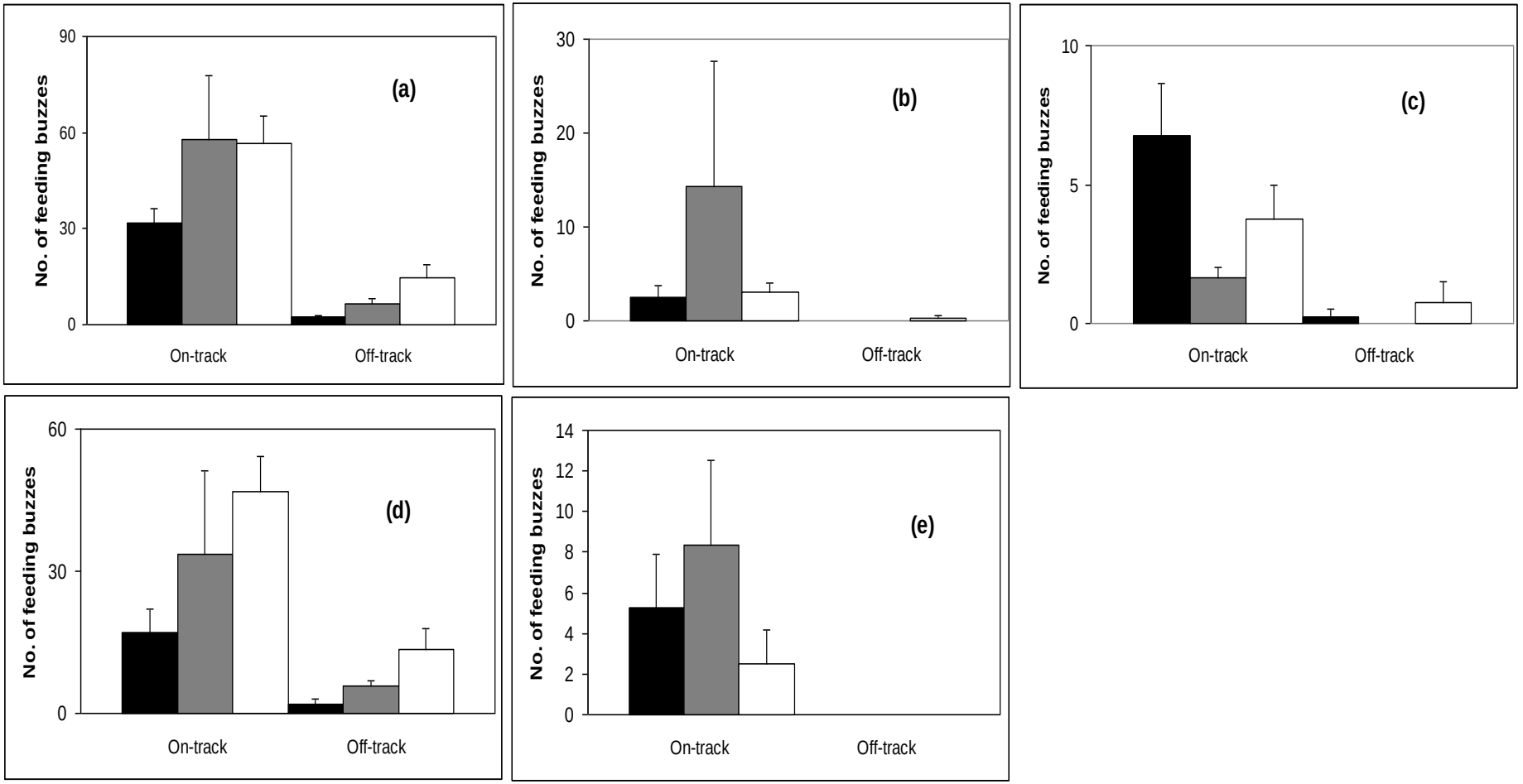
(a)
No. of feeding buzzes
90
60
30
0
On-track
Off-track
(b)
No. of feeding buzzes
30
20
10
0
On-track
Off-track
(c)
No. of feeding buzzes
10
5
0
On-track
Off-track
(d)
No. of feeding buzzes
60
30
0
On-track
Off-track
(e)
No. of feeding buzzes
14
12
10
8
6
4
2
0
On-track
Off-track

Fig. 3.4. Differences in feeding activity (proportion of feeding passes per night: untransformed mean ± SE) in three logging histories (same key as Fig. 3.2), on-track and off-track for (a) overall feeding buzzes; (b) *Chalinolobus gouldi*; (c) *C. morio*; (d) *Vespadelus regulus*; (e) *Falsistrellus mackenziei*. Note that y-axis values vary between species.

Table 3.2. *F*-values from repeated measures ANOVAs for effects of logging history and detector position on bat feeding buzzes, with year as within factor, and logging history and detector position as between factors. Significant results are denoted by asterisks and interactions are not presented as all were non significant.

Species	**Logging history (LH) ($F_{2, 16}$)**	**Detector position (DP) ($F_{1, 16}$)**	**Year (Y) ($F_{1, 16}$)**
Overall feeding activity	7.38**	79.55***	2.10**
Chalinolobus gouldii	0.08	23.03***	0.16
Chalinolobus morio	2.48	39.38***	4.81*
Falsistrellus mackenziei	0.47	20.45***	3.52
Vespadelus regulus	12.80***	41.31***	4.49*

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

BAT ACTIVITY AND VEGETATION CLUTTER

Vegetation clutter indices explained significant amounts of the variation in number of overall bat passes in 2007 (Adjusted $R^2 = 0.51$, $P < 0.001$) and 2008 (Adjusted $R^2 = 0.53$, $P < 0.001$), as well as in numbers of passes by *V. regulus*, *C. morio* and *Nyctophilus* spp. in both years. Increasing understorey clutter was negatively correlated with overall bat activity ($t_{19} = -4.81$ and -4.47, $P < 0.001$), as well as *V. regulus* ($t_{19} = -4.57$ and -5.49, $P < 0.001$), *C. morio* ($t_{19} = -3.22$ and -2.39, $P < 0.01$ and $P < 0.05$) and *Nyctophilus* spp. ($t_{19} = -5.24$ and -5.69, $P < 0.001$) activity. Overstorey clutter was not significantly correlated with effect on either overall or individual species activity.

Vegetation clutter indices were significantly correlated with feeding buzzes in both 2007 (Adjusted $R^2 = 0.39$, $P < 0.01$) and 2008 (Adjusted $R^2 = 0.51$, $P < 0.001$) with increasing overstorey and understorey clutter negatively related to overall feeding buzzes in 2007 ($t_{19} = -3.21$; $P < 0.01$ and $t_{19} = -2.33$; $P < 0.05$, respectively) and 2008 ($t_{19} = -4.47$; $P < 0.01$ and $t_{19} = -2.07$; $P = 0.05$). *Chalinolobus gouldii, C. morio,* and *V. regulus* feeding buzzes were significantly negatively related to vegetation clutter in both years.

LOGGING HISTORY, INSECT BIOMASS AND BAT ACTIVITY

We collected *c*. 8900 insects, with Lepidoptera, Coleoptera and Diptera comprising 86% of trapped individuals. Logging history significantly influenced total dry insect and dry Lepidoptera biomass, with old regrowth recording significantly higher biomasses than other logging histories (Table 3.3). Conversely, logging history had no influence on either biomass of other insect orders, total abundance or abundances of individual orders.Neither total dry insect nor dry Lepidoptera biomass explained significant amounts of variation in overall batpasses in 2007 (Adjusted $R^2 = 0.77$, $P = 0.180$) or 2008 (Adjusted $R^2 = 0.04$, $P = 0.273$), or

numbers of passes of individual bat species. There was no significant interactive effect between vegetation clutter and either total dry insect or dry Lepidoptera biomass on overall bat activity. There was also no significant interaction effect of vegetation clutter and either total dry insect or dry Lepidoptera biomass on individual species activity.

Table 3.3. Results of repeated measures ANOVA for effect of logging history on insect dry biomass, with year as within factor, and logging history as between factor. Significant results are denoted by asterisks and interactions are not presented as all were non significant.

	Logging history (LH) ($F_{2, 37}$)	**Year (Y) ($F_{1, 37}$)**
TDIB	3.39*****	1.30
Lepidoptera	4.23*****	7.50******
Coleoptera	1.22	1.47
Diptera	0.47	0.46
Hymenoptera	2.01	3.93
Blattodea	1.26	0.05
Mantodea	1.13	1.47
Hemiptera	1.32	3.65
Trichoptera	0.81	0.12

*$P < 0.05$; **$P < 0.01$

3.4 Discussion

This is the first study to relate bat and insect activity to logging history. We found old regrowth forests supported greater bat and insect activity, but lower vegetation clutter, than either young regrowth or recently logged forest. Forest tracks across all logging histories provided important habitat for most bat species. Although tracks were a small proportion of forest landscapes, they facilitated access and use of otherwise inaccessible young regrowth and have the potential to reduce logging impacts on bats.

METHODOLOGICAL LIMITATIONS

We sampled bat activity using Anabat detectors which have biases in their effectiveness, as not all species are detected equally. Some, such as *Nyctophilus* spp., that emit low amplitude calls which attenuate rapidly (Neuweiler 1989), may be under-represented in detector-based surveys (e.g. Barclay 1999). Furthermore, bat detectors do not measure abundance but activity, so that our conclusions on relative habitat use should be supported by population studies (e.g. on marked individuals). Additionally, vegetation can affect detectionranges, but we minimized this effect by facing detectors into forest gaps or along tracks (Law & Chidel 2002; Patriquin & Barclay 2003). Lastly, we used light traps to sample insect prey, but their efficacy varies between taxa (Bowden 1982), sampling only taxa attracted to light. Thus, our results represent a portion of the overall insect community available to bats.

IMPACT OF LOGGING ON ACTIVITY OF BATS

Overall bat activity and feeding buzzes were 47% and 45% higher in old regrowth than young regrowth and logged forest, respectively, suggesting that bats foraged more in old regrowth sites. This result was driven by *Vespadelus regulus* and *Nyctophilus* spp. activity, as these species dominated the community. *Nyctophilus* spp. was only affected by logging history in

2008, although why their response differed between years is unknown. Previous studies have demonstrated lower bat activity in cluttered regrowth forest compared with more open, unlogged forests (e.g. Brown, Nelson & Cherry 1997; Menzel *et al*. 2002). Indeed, a negative relationship with understorey clutter was the most consistent predictor of total bat activity in our study, indicating that low bat activity in young regrowth and logged forest was probably related to high understorey clutter at these sites, which probably both interferes with ultrasonic signals and reduces access to prey items (Rainho, Augusto & Palmeirim 2010).

One major finding was that on-track locations had similar activity levels and feeding buzzes across logging histories, suggesting tracks provide suitable commuting and foraging habitat for bats within logged forests. This is consistent with data from eastern Australia, where similar bat activity levels were reported on tracks through regrowth and old growth (Law & Chidel 2002; Lloyd, Law & Goldingay 2006). Tracks cutting through young regrowth create internal edges, allowing bats greater access to sections of young regrowth forest. Although tracks represented a small portion of the landscape (*c*. 1%), which limits the area that bats can access, the high number of feeding buzzes on-tracks, compared to off-track sites, in young regrowth suggests that tracks were important in making sections of otherwise unsuitable habitat available for foraging. Our results add to studies demonstrating that tracks traversing logged forests are used by many bat species (Law & Chidel 2002; Lloyd, Law & Goldingay 2006) and emphasize the importance of linear elements, including tracks (e.g. Menzel *et al*. 2002; Adams, Law & French 2009), hedgerows (Walsh & Harris 1996), riparian creeklines (Lloyd, Law & Goldingay 2006) and coupe edges after logging (Morris, Miller & Kalcounis-Rüppell 2010), to bats. Furthermore, some radiotracking studies have demonstrated that some species roost and forage in regrowth forest (e.g. Law&Anderson 2000).

We found that neither insect biomass nor the interaction effects of vegetation clutter and insect biomass significantly affected bat activity. This suggests that food availability, at least in terms of sampled insect biomass, did not affect bat activity over the range of vegetation clutter sampled. This contrasts with studies which found positive correlations between bat activity and insect abundance (e.g. Hayes 1997) or correlations only where vegetation was relatively open (Adams, Law & French 2009). However, these studies are not directly comparable as they either did not consider temperature as a factor influencing bat and insect activity, or sampled insect abundance using light traps concurrently with bat sampling (Adams, Law & French 2005). Adams, Law & French (2005) sampled insects on- and off-tracks whereas we only sampled off-tracks and so vegetation may have been too cluttered for bats to exhibit higher activity where insects were more common. Thus, although our study indicated that food resources did not explain differences in bat activity, it is unclear whether this lack of agreement with other studies is real or due to methodological differences.

In addition to lower clutter, many bats preferentially roost in mature forests with abundant hollow-bearing trees (e.g. Kalcounis- Rüppell, Psyllakis & Brigham 2005), which could explain high bat activity in old regrowth forest in this study. Furthermore, many temperate tree-roosting bats switch roosts often (e.g. Willis & Brigham 2004) and bats typically roost in different trees within the same general area (e.g. Brigham *et al*. 1997; Cryan, Bogan & Yanega 2001). A concurrent radiotelemetry study revealed that bats preferred roosting in older forest (Webala *et al*. 2010), therefore, although bats may take advantage of greater foraging opportunities at off-track sites in old regrowth, many bat species also roost there (Kunz & Lumsden 2003).

IMPACTS OF LOGGING ON INDIVIDUAL SPECIES

Different bat species respond differently to logging and resulting changes in vegetation structure (e.g. Law & Chidel 2001), depending onmorphology and plasticity in foraging behaviour (Bullen & McKenzie 2001). Species with low aspect ratios are more manoeuvrable than those with high aspect ratios, which forage exclusively in open habitats because they cannot negotiate cluttered habitats (Humes, Hayes & Collopy 1999). With differing aspect ratios among jarrah forest bats, we recorded a range of responses to logging. Logging history significantly affected *V. regulus* and *Nyctophilus* spp. activity, with activity for both greater in old regrowth than other logging histories. Law & Chidel (2001) reported similar findings for *V. regulus* in New South Wales, Australia, with highest activity in unlogged forests. With a moderate aspect ratio (Fullard *et al*. 1991), and relatively high flight speeds, *V. regulus* is a clutter-sensitive species which cannot forage efficiently in highly cluttered regrowth. Indeed, the understorey clutter index explained significant amounts of variation in V. *regulus* activity, suggesting that clutter negatively affected its off-track activity. Conversely, *V. regulus* activity on-tracks did not differ among logging histories, underscoring the importance of tracks as an ameliorative measure in regrowth forest for less manoeuvrable species (Law & Chidel 2002).

Our finding of highest *Nyctophilus* spp. activity in old regrowth in 2008 contrasts with Law & Chidel (2001, 2002) who reported similar *N. gouldi* activity in cluttered regrowth and unlogged forest. *Nyctophilus* species have low aspect ratios and wing loadings, lower than other species in south-western Australia, allowing slow flight and high manoeuvrability (Fullard *et al*. 1991) so they should be themost clutter-tolerant species. Thus, activity was expected to be higher off-track, compared with on-track locations, not lower as we found. This most parsimonious explanation is that post-logging jarrah forest regrowth is more

cluttered than the forests studied in New South Wales. High *Nyctophilus* activity on-track, nonetheless, supports previous observations that such 'clutter-tolerant' bats are not confined to cluttered areas for foraging, but routinely use open habitats as well (e.g. Schnitzler & Kalko 2001).

As predicted from ecomorphology, larger species (*C. morio*, *C. gouldii*, F. *mackenziei*) generally avoided regrowth and were more active on-tracks. With high aspect ratios and wing loadings, *Tadarida australis* and *Mormopterus* species 4 are the most clutter-sensitive south-western Australian bats (Fullard *et al*. 1991), and probably avoided clutter by only utilizing open areas. These fast-flying molossids were recorded infrequently on-track and most probably flew above the canopy. However, as ground-based Anabat detectors can readily pick up molossid calls from above the canopy (Herr & Klomp 1997), we suggest that these bats occur in low numbers at our forest sites.

SYNTHESIS AND APPLICATIONS

We found that old regrowth provided better quality habitat than other logging histories, leading to higher overall and foraging bat activity. Conversely, young regrowth forest recorded the least bat activity and appeared to provide less suitable habitat for many bat species. Since 1985, logging practices in jarrah eucalypt forests have changed to employ selective logging methods as a more ecologically sustainable operation. Current management practices seek to achieve overstorey structural diversity at operational and landscape scales through the establishment of formal and informal reserves and retention of habitat elements in harvesting operations (CCWA 2004). Our study demonstrated that tracks have some potential in ameliorating logging impacts on bats.However, unlogged buffers, compared to forest tracks, constitute a much greater proportion of the jarrah forest landscape, and appeared better

at ameliorating logging impacts on bats. Unlogged buffers provided multiple roosting opportunities for bats because they contained higher densities of hollow-bearing trees than post-logging forests (Webala *et al*. 2010) and also provided forests with low or moderate clutter that appeared to be high quality foraging habitat. With *c*. 39% of the study area permanently closed to logging, these measures

should increase the availability of open spaces and edges required bymany foraging bat species (Law & Chidel 2002), as well as provide roost trees (Lunney *et al*. 1988; Brigham *et al*. 1997). However, the amount of unlogged area that needs to be retained for bat population persistence requires further research. Insummary, we believe that the retention of unlogged areas within logged landscapes provides the best solution to maintaining bat populations in production forests and is likely to be themost important strategy in achieving ecologically sustainable forestmanagement for bats inmany forest ecosystems.

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Chapter 4

Roost site selection by Southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi* in logged Jarrah forests, south-western Australia

Published in *Forest Ecology and Management*

Plate 4.1. An alert Gould's Long-eared Bat (*Nyctophilus gouldi*).

Photo: Kellie Patterson / Paul Webala

Plate 4.2. The southern forest bat (*Vespadelus regulus*) in flight.

Photo: Joe Tonga / Paul Webala

Plate 4.3. The *Nyctophilus gouldi* roost located under the skirt of a balga grass tree.
Photo: Carole Patterson / Paul Webala

Plate 4.4. Female *Nyctophilus gouldi* roost located in hollow in a burnt jarrah log, March 2008

Abstract

Information on roosting requirements and responses to forest management is integral to effectively conserve and manage bat populations. Tree hollows are especially important for roosting bats given the long time taken for hollows to form. We used radiotelemetry to compare roost site selection in two species, *Vespadelus regulus* and *Nyctophilus gouldi*, in logged jarrah forests of south-western Australia. We compared characteristics of roost trees and forest structure around roost trees (n = 48) with randomly located plots at a local roost tree level (n = 90) in February and March 2009. For landscape features, we compared roost trees with randomly selected trees in the broader landscape that had cavities or exfoliating bark (n = 204). *V. regulus* roosted solely in hollows that were located predominantly in contemporarily unlogged buffers and mature forest while *N. gouldi* used a broader range of roost types, located in contemporarily unlogged buffers and mature forest and in retained habitat trees in gap release and shelterwood creation silvicultural treatments. In contrast with *N. gouldi*, which selected hollows or crevices under bark near the ground and close to vegetation, *V. regulus* used hollows that were high above ground and had little surrounding vegetation. Both species preferred large trees, in intermediate or advanced stages of decay and crown senescence. Bats changed roosts frequently, with short distances between subsequent roosts, suggesting a degree of spatial fidelity. Contemporarily unlogged buffers and mature forest contained higher densities of trees with hollows than gap release and shelterwood creation areas, potentially providing more alternate bat roosts. Our results demonstrate the importance of mature forest and unlogged buffers as bat roost sites in logged jarrah forests of south-western Australia, but the area of old forest required by these and co-occurring bat species remains to be determined.

4.1 Introduction

The management of wildlife populations requires an understanding of how individuals use their habitat, and this knowledge is particularly important for the conservation of threatened or declining species. One group that appears to be in global decline are bats (Hutson *et al*., 2001) yet, for many bat species, very little is known about how they use their habitat or their sensitivity to habitat modification. This information is, however, critical if bats are to be successfully conserved and managed. One major threat facing bats worldwide is timber harvesting (Hutson *et al*., 2001) and the destruction and alteration of roost sites is thought to be one of the main way that timber harvesting impacts on bat populations. Therefore, in areas where timber harvesting occurs, it is critical that we understand the roosting requirements of bats if we want to effectively conserve and manage bat populations.

Conservation of roost sites is critical if bat populations are to be conserved and maintained because bats spend a large portion of their life in roosts and use them for a wide variety of important functions. These functions include as diurnal shelter, maternity, bachelor, migrating, and hibernation sites (Kunz and Lumsden, 2003). Roost sites can also facilitate complex social interactions, including information transfer, act as breeding sites for rearing young and mating (Kunz, 1982; Willis and Brigham, 2004), offer protection from inclement weather, minimize parasite load (Lewis, 1996), promote energy conservation and reduce predation risks (Rydell *et al*., 1996; Vonhof and Barclay, 1996; Turbill *et al*., 2003; Turbill and Geiser, 2005; Turbill, 2006). As only a few bat species are known to manipulate the physical structure of their roosts, the survival and reproductive success of bats is strongly influenced by the type and location of existing roosts present in an area (Racey and Swift, 1981; Brigham and Fenton, 1986; Vonhof and Gwilliam, 2007).Therefore, the maintenance of existing roost sites is important for the survival of bat populations.

Timber harvesting, as well as forest clearing and fragmentation, typically leads to a reduction in numbers of large live and standing dead trees (Laurance *et al*., 2000; Gibbons *et al*., 2008; Oliveira *et al*., 2008). In Australia, this situation is manifested in the loss of older trees, which may threaten the survival and persistence of bats and other vertebrate wildlife dependent on this resource (Lunney *et al*., 1988; Lindenmayer and Franklin, 2002; Lunney and Matthews, 2004). The importance of large, hollow-bearing trees as roosts for many bats is well documented in the literature (Taylor and Savva, 1988; Hosken, 1996; Law, 1996; Law, 2004). More than 50% of Australia's insectivorous bats roost and breed in tree hollows (Tidemann and Flavel, 1987; Churchill, 2008) with large hollows being particularly important for maternity roosts (Law and Anderson, 2000; Lumsden *et al*., 2002*a*). Large, hollow-bearing trees also provide exfoliating bark and bark fissures, which are also important roost sites for some bat species, at least for part of the year (Goldingay, 2009). These species include *Nyctophilus bifax* (Lunney *et al*., 1995), *N. geoffroyi* (Taylor and Savva, 1988; Lumsden *et al*., 2002*a*), *N. gouldi* (Lunney *et al*., 1988; Tidemann and Flavel, 1987) and *N. timoriensis* (Churchill, 2008), but, even in these species maternity roosts typically occur in tree hollows (e.g. Lunney *et al*., 1988; Lumsden *et al*., 2002*a*; Goldingay, 2009), highlighting the importance of tree hollows as key resources for bats.

Hollows may provide optimal microclimates for maternity roosts because they are better insulated against inclement weather than roosts under bark (Sedgeley, 2001; Lumsden *et al*., 2002*a*). Such hollows are more likely to occur and be used by bats in large trees that are many centuries old (e.g. Mackowski, 1984; Gibbons *et al*., 2000; Lindenmayer *et al*., 2002; Whitford, 2002; Smith *et al*., 2008) and the time required for a tree to develop hollows that are suitable for use by fauna is generally much longer than the time between timber-harvesting events in production forests (e.g. Ball *et al*., 1999; Whitford, 2002; Whitford and

Stoneman, 2004). The lag times thus make bats vulnerable, given the short logging rotations prevalent in Australia (Parnaby and Hamilton-Smith, 2004). Consequently, many bat species may be negatively impacted by the removal of large and older trees during logging, which leads to a reduction in the number of suitable roost sites and possibly render roost sites in remaining trees suboptimal (Goldingay, 2009).

Information on the dependence of birds and non-volant mammals on hollows in older trees in Australia is more extensive (e.g. Abbott and Whitford, 2002; Gibbons and Lindenmayer, 2002) than our knowledge of bat requirements. Various management prescriptions in production forests are intended to mitigate impacts on hollow-roosting species, including retention of old-growth habitat, riparian buffers and other unlogged reserves (see Lindenmayer and Franklin, 2003) and the retention of hollow-bearing trees within logged forests (CCWA, 2003). Riparian zones have been shown to provide foraging and drinking habitat (Law and Chidel, 2002; Lloyd *et al*., 2006), as well as roosting habitat (Lunney *et al*., 1988, Taylor and Savva, 1988; Law and Anderson, 2000; Schulz, 2000), for many bats, however, it remains to be determined whether bats use either the retained unlogged habitat or the retained hollow-bearing trees after logging. Furthermore, whether unlogged habitat patches are sufficiently large to allow for temporal changes in roost requirements, or how much unlogged habitat is enough for the long-term persistence of bats remains to be determined (Law, 1996).

Whereas a number of studies have investigated roosting requirements of bats, especially in eastern Australia (e.g. Taylor and Savva, 1988; Lunney *et al*., 1988, 1995; Law and Anderson, 2000; Lumsden *et al*., 2002*a*), there is a general dearth of information regarding impacts of roost-site reductions on the survival of a wide range of bat species in other areas of

Australia, including Western Australia. Furthermore, temporal and spatial changes in the use of hollows and crevices under exfoliating bark by particular species have not been examined. Yet, to verify effective management, there needs to be a sound knowledge of both the specific requirements of each bat species and the availability of roost types (bark, hollows, etc., Goldingay, 2009). While bats make up a significant proportion of the mammal fauna in the jarrah forest of south-western Australia (9 of around 30 native extant species), little is known about their roosting requirements or their responses to the removal of suitable roost sites, and it is unclear whether we can extrapolate results from eastern Australia. We investigated the potential sensitivity of two sympatric species of jarrah forest-dwelling vespertilionid bats, the southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi*, to the loss of roost sites from recently logged forests and the effectiveness of current management practices at conserving appropriate roost sites. The two species were selected because they have small home ranges and were, therefore, logistically easier to track to their day roosts. Furthermore, these species display different wing morphologies and echolocation call attributes, both potentially influencing how each species uses a logged landscape. Although some studies describe the roost requirements of *N. gouldi* elsewhere (Lunney *et al*., 1988; Turbill, 2006), little is known about the roosting requirements of *V. regulus*, although Taylor and Savva (1988) tracked two female *V. regulus* bats to four roost hollows in live and dead Eucalypt trees in Tasmania.

To better understand the roosting-habitat requirements of the two species as influenced by logging, we studied inter-specific patterns of roost-site selection. Based on previous studies on the same or congeneric species (e.g. Lunney *et al*., 1988; Herr and Klomp, 1999; Law and Anderson, 2000; Campbell *et al*., 2005), we predicted that roost trees of the two species would be larger and less cluttered by surrounding vegetation than random trees. Our study

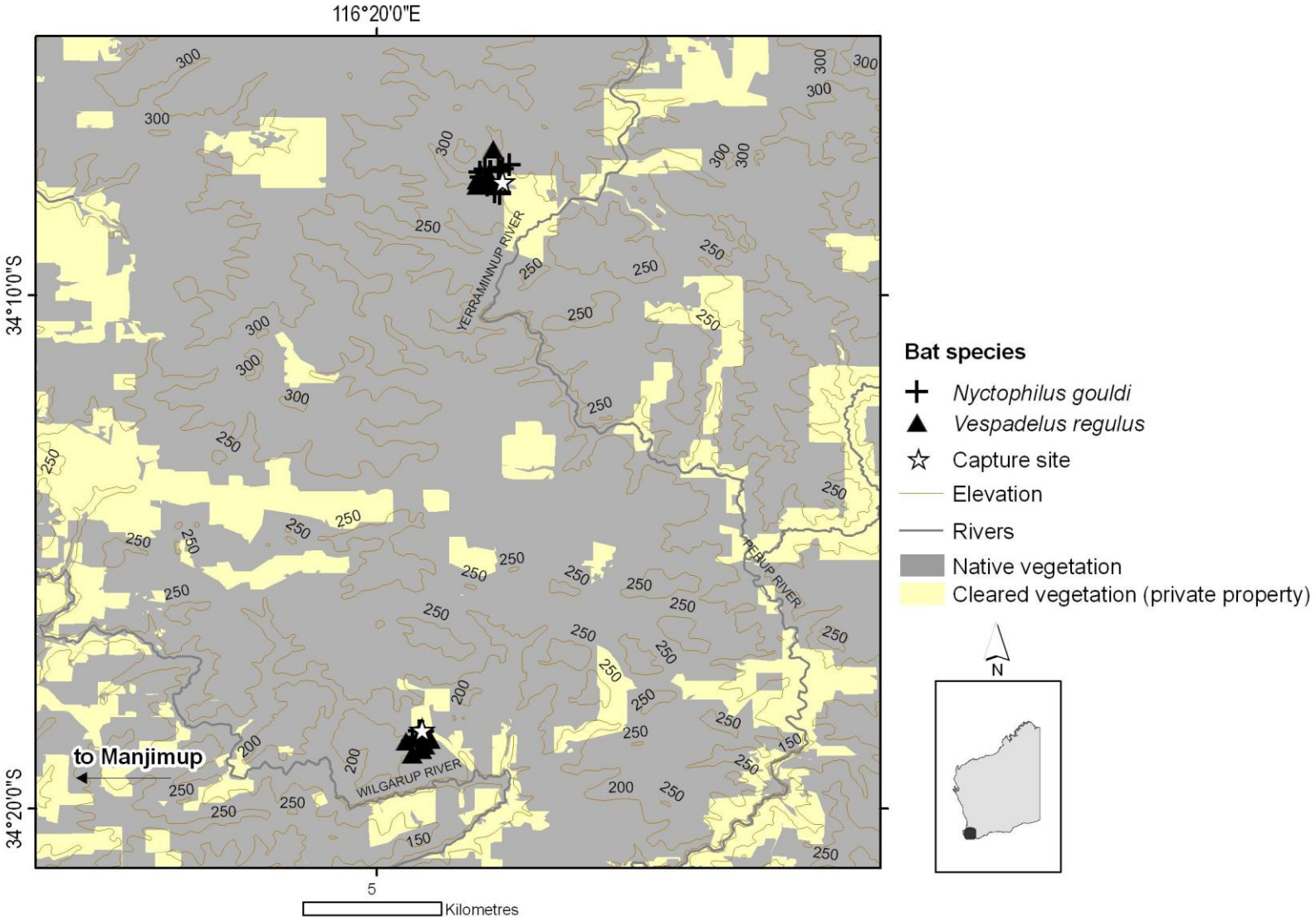
objectives were to (1) investigate roost and site selection by bats in logged forests by comparing roost trees (and the surrounding habitat) with potential roost trees and surrounding plots to identify important roost habitat characteristics; (2) compare roost and site characteristics of *N. gouldi* with those of *V. regulus*; and (3) determine the relative importance of buffer zones and other unlogged areas as roosting habitat for bats in logged jarrah forests, south-western Australia.

4.2 Methods

STUDY AREA

The study was conducted east of Manjimup and Bridgetown in the southern jarrah forest of Western Australia (Fig. 4.1a, b and c). The area has a Mediterranean-type climate with cool, wet winters and warm summers (Gentilli, 1989). Monthly average minimum and maximum temperatures respectively vary from 5.7 to 12.9ºC and 15.5 to 27.6ºC. Annual average rainfall at Manjimup and Bridgetown is 1011.8mm and 829.4mm respectively, with over 70% falling between May and September at both locations.

The study area was primarily jarrah forest interspersed with some patches of farmland. Jarrah forest is a dry sclerophyll forest type where jarrah (*Eucalyptus marginata* Donn. ex. Smith, 1802) is the dominant tree with marri (*Corymbia calophylla* K. D. Hill and L. A. S. Johnson) also common in many areas. Understorey species richness is generally high (Havel, 1975*a*, *b*; Commonwealth of Australia and Western Australian Government, 1998). Typical midstorey species include jarrah, marri and bull banksia (*Banksia grandis*). Common understorey plants include *Acacia pulchella, Bossiaea ornata, B. linophylla, Hakea lissocarpha, Leucopogon capitellatus, L. verticillatus, L. propinquus, Lomandra* sp., *Macrozamia riedlei, Myoporum* sp., *Persoonia longifolia, Xanthorrhoea gracilis* and *X. preissii*.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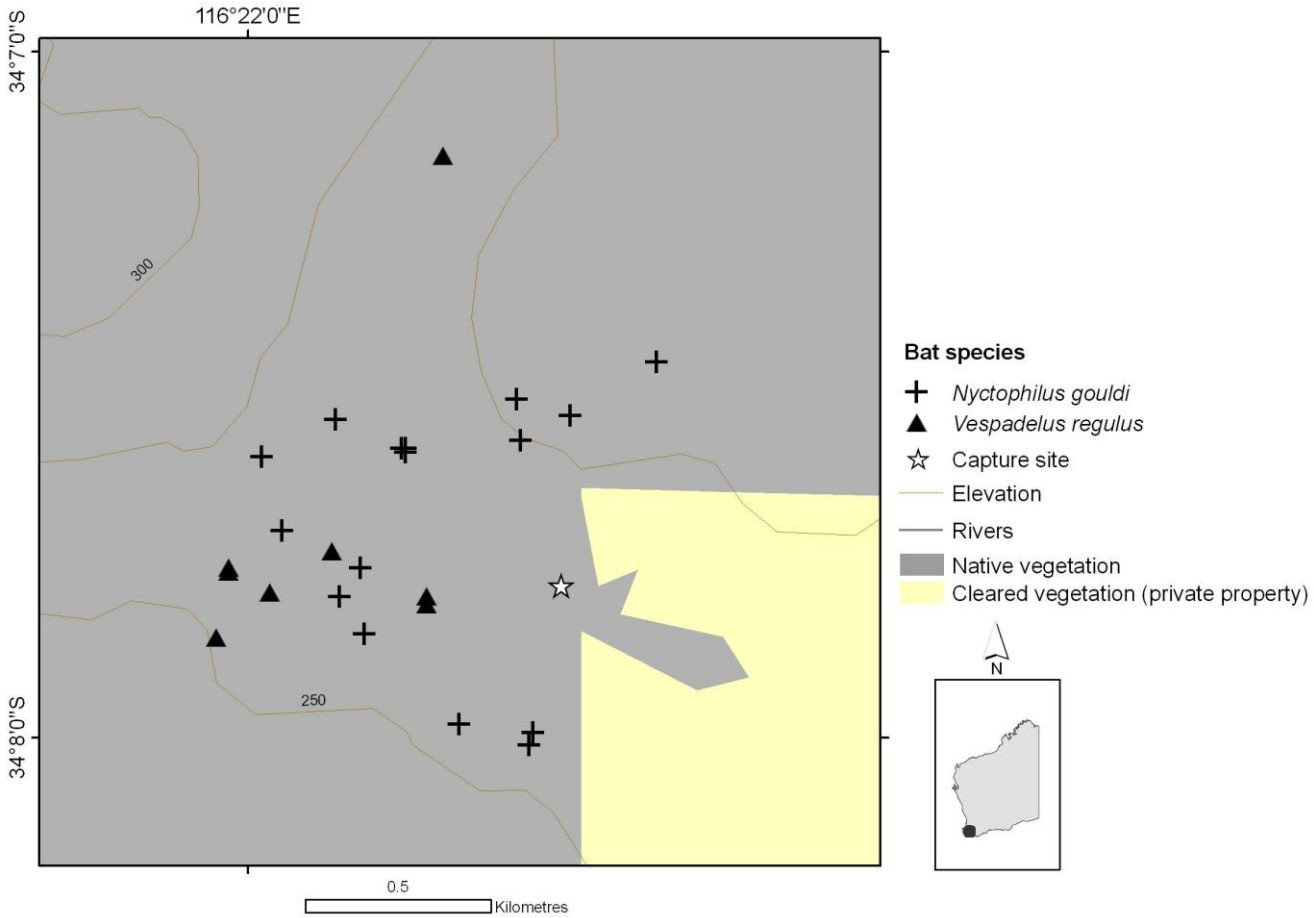
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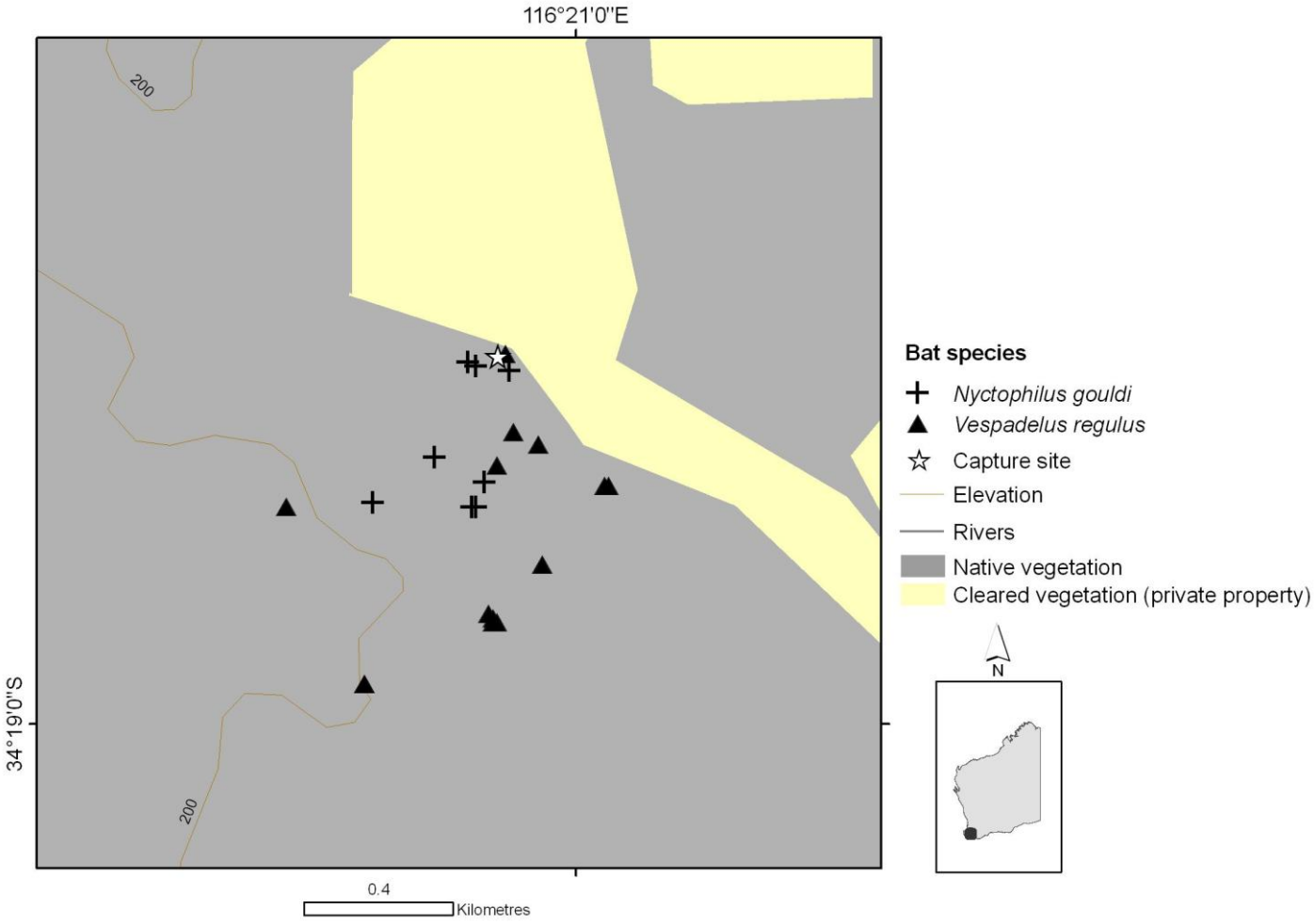
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N

(c)

Fig. 4.1. ***a***. General map showing bat roost and capture sites. Inset shows the location of the study area within Western Australia. ***b***. Map showing bat roost sites at the northern capture site of the study area. Inset shows the location of the study area within Western Australia. ***c***. Map showing bat roost sites at the southern capture site of the study area. Inset shows the location of the study area within Western Australia.

LOGGING HISTORY

A description of the history of logging in the jarrah forest is given by Abbott and Loneragan (1986), Stoneman *et al*. (1989) and Bradshaw (1999), including how logging practices have changed over time. The current methods have been in place since 1985 and include: (1) 'Gap Release', involving the removal of about 95% of mature overstorey to provide opportunity for a regenerating tree cohort, with four to five habitat trees (those with characteristics that give them a high probability of containing hollows suitable for fauna) and six to eight potential habitat trees retained per hectare; and (2) 'Shelterwood Creation' involving the retention of 40 to 60% of basal area after logging to provide seed for regeneration. Gaps are ≤ 10 hectares in size, variable in shape and do not extend across ridges while shelterwoods have no size limitation and can extend across ridgelines. Buffers of unlogged forest between gap release patches and along riparian areas, including streams and creeks, are also designated within logged areas. Other areas excluded from logging include diverse ecotype zones, road reserves, uneconomic areas, old growth forest, native forest retained for research purposes, and fauna habitat zones.

Much of the study area (Kingston and Warrup Forest blocks) has experienced at least one cycle of timber harvesting since about 1920. Only about 6% is recorded as not having been logged. About 20% of the total area has been logged since 1980 constituting at least the second time these particular stands have been harvested: generically referred to here as 'regrowth' forest. The remainder of the area (74%) was last harvested prior to 1980, when logging operations characteristically removed smaller timber volumes and were variable both spatially and temporally (Bradshaw 1999). Referred to here as 'mature' forest, these areas tended to be selectively harvested, thereby retaining many of the characteristics of a mature

stand including a relatively greater abundance of large trees and a relatively more open understorey and midstorey compared with more recently logged areas.

FIELD METHODS

Bats were initially captured in February and March 2009 using harp traps (Two-Bank 4.2 square metres; Austbat Research Equipment, Victoria) at two different water holes within different logging histories (Fig. 4.1a, b and c). Data collected from each captured bat included species, age (juvenile, subadults, adults), sex, mass (to nearest 0.2g using Pesola spring scales), and reproductive condition. We determined female reproductive condition by palpating the abdomen and inspecting the mammae and determined age-class by examining the degree of epiphyseal-diaphyseal fusion (Racey, 1988). Individual bats of both species were radio-tracked by attaching miniature position-sensitive single-stage radio transmitters with 18-20cm antenna attached to the dorsal fur using Superglue. Transmitters weighing 0.40 g - 0.43 g (Titley Electronics, Ballina) were fitted to *Nyctophilus gouldi* bats and others weighing 0.36 g - 0.40 g (Holohil Systems Ltd., Woodlawn, Ontario, Canada) were fitted to *Vespadelus regulus* bats.

For *N. gouldi*, transmitters weighed less than the 5% body mass guideline in which transmitter weight can influence flight performance (Aldridge and Brigham, 1988). However, for *V. regulus*, transmitters weighed 5 – 8% of body mass. Other studies have successfully radio-tracked microbats with transmitters representing at least 8 % of body mass (e.g. Lunney *et al*., 1995; Law and Anderson, 2000; Lumsden *et al*., 2002*b*; Campbell *et al*., 2005).

Bats were monitored using Australis 26k Scanning Receivers and AY/C Yagi 3 element collapsible hand-held antennas. We tracked individual bats to their day roosts on consecutive

days until transmitters dropped off or the battery failed (ca. 12 days; n = 23). Attempts were made to observe roost entrances at dusk to determine the exact type and location of the roost in the tree and the colony size. To estimate local roost availability, a 0.03 ha circular plot (10-m radius) was marked and centred on the roost tree (Vonhof and Barclay, 1996). The species of the roost tree, logging history and the geographical location (using GPS) of the site were recorded. A variety of roost tree and site characteristics were then measured (Table 4.1).

To estimate roost availability in the surrounding forest landscape, a sample of random trees were measured for comparison with roost trees and an additional plot established around these randomly selected trees. At the local roost tree scale, this plot was located by selecting a random point between 100 m and 300 m from the roost tree in a randomly selected direction (Vonhof and Gwilliam, 2007). From the random point, one random tree was selected from a sample of four trees from the four compass directions, and a plot was marked around this random, focal tree. Only trees with DBHOB ≥ 20 cm and with at least one observable hollow or peeling bark were selected. The tree and site characteristics of the focal tree were measured as for roost trees. For comparison of landscape features of roost trees with random trees at the landscape scale, mature trees (DBHOB ≥ 80 cm; Lunney *et al*., 1988) with at least one observable hollow and/or peeling bark were selected randomly in 10 50x50 m plots in each of the following logging histories; gap release, shelterwood creation, gap buffers, riparian buffers and mature forest. These plots were also used to estimate the density of trees with hollows and/or peeling bark in the landscape.

Table 4.1. Variables measured for the roost sites of the Southern forest bat (*Vespadelus regulus*) and Gould's Long-eared Bat (*Nyctophilus gouldi*) and comparative random sites in the jarrah forests, south-western Australia. Random trees were measured both locally around roost trees and in the broader forest landscape.

Variable	**Category/Measurement (units)**
Roost variables	Identification from leaf/bark characteristics
Diameter at breast height (DBHOB)	Using measuring tape at 1.3m over bark
Height (m)	Measured using Tree Vertex
Height relative to canopy height (m)	Difference in roost tree and the canopy height. Canopy height measured as below
Snag class (decay stage)	1 = all live tree; 2 = <30% dead; 3 = >30% dead; 4 = 100% dead (Maser *et al*., 1979; Campbell *et al*., 2005)
Percent bark cover (bark-cover class)	1 = none; 2 = <10 percent, 3 = 10-25 percent; 4 >25 percent
Crown senescence classification	Assessment of crowns as better (SENES0) or worse (SENES 9 and 10) (Whitford, 2002)
Dead Branch Order (DBO)	Scale of assessing DBO (DB1 to DB9). DB9 is a tree trunk more deteriorated than DB8 (Whitford, 2002)
Location	Recorded using GPS
Distance from previous roost, if any (m)	Straight-line distance generated from differential GPS
Distance from capture site	Straight-line distance generated from differential GPS
Roost variables	
Roost type [a]	Hollow, under bark, fissure, other
Roost entrance height [a]	Identified the cavity/bark occupied by assessing radio-signal strength and direction when standing near the tree. Measured height using Tree Vertex
Site variables (extrinsic variables)	
Distance to nearest 5 available trees (m)	Measured using Laser Rangefinder for trees ≥ 20 cm DBHOB in 0.03-ha plot
Height of available nearest tree (m)	Measured using Tree Vertex for nearest tree ≥ 20 cm DBHOB in 0.03-ha plot
Mean Canopy height (m)	Four randomly selected trees within plot or extra trees measured as required using Tree Vertex
Mean canopy cover	Four densiometer readings, 90^{o} apart, at each plot, 25m from the roost tree
Vegetation clutter indices [b]	Foliage cover scores for the upper stratum (≥ 15m), mid-storey stratum (5 -15m), woody-seedling (shrubs) stratum (0.75cm - 5m) and herbaceous groundlayer stratum (0 – 0.75cm): - 1 = very sparse (0-5%); 2 = sparse (5-25%); 3 = moderate (26-50 percent); 4 = mid dense (51-75%); 5 = dense (≥ 75%).
Slope (degree)	Obtained from GIS data of the study area
Elevation (m)	From GIS data of the area
Distance to nearest water point	Distances obtained from GIS data of the study area
Distance to nearest creek line or watercourse	From GIS data
Distance to nearest gap or shelterwood	From GIS data

[a] Only measured for roost trees; [b] Each stratum score was weighted (multiplied) by its height to get the final clutter index for that stratum (Law and Chidel, 2002).

STATISTICAL ANALYSES

All variables were continuous or rank ordered (Table 4.1). Data from five *N. gouldi* roosts (blackbutt *Eucalyptus patens*; $n = 3$ and balga *Xanthorrhoea preissii*; $n = 2$) were not considered in the analysis of roost characteristics because of small sample sizes. We analysed data for marri and jarrah roost trees separately, to account for the structural differences between the two tree species, since these were predominantly selected as roost sites.

Tree, roost and site variables were initially compared using Spearman rank correlations. Where pairs of variables had correlation coefficients greater than 0.8, one of the pair was excluded from further analysis. For instance, to test for differences in clutter levels between roost and random plots, we first determined relationships between clutter indices for each stratum. Ground, shrub and mid-storey indices were highly correlated with each other ($0.81 < r < 0.84$, $P < 0.001$), but none were correlated with canopy clutter, thus, in analyses, the three sub-canopy indices were summed together, resulting in only two, the sub-canopy and the canopy indices (Table 4.1).

Roost trees used by each species (*V. regulus* and *N. gouldi*) were compared to random trees to test whether they were distinct from the local and landscape population of available trees. Direct inter-specific comparisons of the characteristics of roost trees were made to investigate species-specific preferences for roost tree and site characteristics. We used the Bray-Curtis association measure to assess similarities among roost and random trees with respect to variables related to tree and site characteristics (Table 4.1). Semi-strong hybrid multidimensional scaling ordination was used to explore relationships and to provide, in a few dimensions, an accurate representation of the similarity between roost and available trees on the basis of their attribute profiles (tree/site characteristics) (Rhodes and Wardell-Johnson,

2006). An Analysis of Similarity (ANOSIM) was then applied to test for the significance of any differences. Mann-Whitney *U*-tests were used to compare means and frequencies of use and availability for roost trees and random trees and site characteristics for both continuous and ordinal variables because data were heteroscedastic A Student's *t*-test was used to test for differences in the distance moved between capture sites and roost trees and between successive roosts, with species as a factor and distances as dependent variables. To compare continuous variables of roost trees used by *V. regulus* with those used by *N. gouldi* after transforming the data using $\log_e(x+1)$, two-sampled *t*-tests were used with species as a factor. Differences between logging histories (gaps, shelterwoods, gap buffers, riparian buffers and mature forest) in the density of trees with hollows were tested using one-way ANOVA with logging history and density as the predictor and dependent variables, respectively. *Post-hoc* Tukey tests were performed to check for significant differences between treatments (Day and Quinn, 1989). Significant results are presented at the level of $P = 0.05$. All means are presented ± SE. These analyses were carried out using Statistica 7.0 (Statsoft, Inc., Oklahoma, USA).

4.3 Results

RADIO-TRACKING

We attached transmitters to 12 *V. regulus* and 11 *N. gouldi* (Table 4.2), of which 64% of *N. gouldi* and 83% of *V. regulus* were females, all nonparous at the time of transmitter attachment. Two transmitters attached to *V. regulus* either failed, or bats could not be located after the first night, while the remaining 10 bats were tracked to 21 different roost trees for a mean of 5.9 ± 1.6 days. For *N. gouldi*, all 11 bats were tracked to 27 different roost trees for a mean of 4.3 ± 0.9 days (Table 4.2). The roosts for both bat species occurred primarily in two

species of trees, jarrah (n = 32) and marri (n = 11). *N. gouldi* also used blackbutt (n = 3) and balga (n = 2) as roosts.

N. gouldi roosts were closer (340.2 ± 59.7 m; n = 11) to capture sites, compared to *V. regulus* (465.5 ± 89.8 m; n = 10) (t_{19} = -2.23; P = 0.038) (Figs. 1a, b and c). Bats changed roosts every 2.8 ± 0.3 (n = 11) and 2.3 ± 05 (n = 10) days for *N. gouldi* and *V. regulus*, respectively. We documented eight cases where individual bats vacated a roost tree for between 2 and 4 days and then returned to that roost tree while still carrying a transmitter (*N. gouldi*, n = 1; *V. regulus*, n = 7). *N. gouldi* moved 164 ± 16 m (n = 16) between consecutive roosts while *V. regulus* moved 400 ± 38 m (n = 13) and this difference was significant (t_{27} = -5.48; P < 0.001).

It was not possible to determine the sex and age structure of bat species within roosts as attempts to trap at one *V. regulus* communal roost failed. However, based on emergence counts (n = 9) at this communal roost, the colony ranged from 10 to 15 individuals over nine days, with a mean colony size of 12.3 ± 0.5 bats. The sex composition of the communal roost could not be determined either, except for the two females with transmitters. In addition, on separate occasions, and in separate balga roosts, 25 and 18 *N. gouldi* bats were counted as they exited after their roosts were disrupted

Table 4.2. Number of transmitters attached to each sex and species of bat, the number never located, number of roosts located and the corresponding number of potential roost trees measured in the jarrah forests, south-west Western Australia. The number of individuals found in one roost is the difference between column 3 and the sum of columns 7, 8 and 9.

Species	Sex	No. of transmitters fitted	No. never located	Total No. of roosts located	Total No. of available trees measured	No. of individuals found in two roosts	No. of individuals found in three roosts	No. of individuals found in ≥ 4 roosts
N. gouldi	F	7	0	19	34	2	3	1
	M	4	0	8	18	2	1	0
	Subtotal	11	0	27	52	4	4	1
V. regulus	F	10	1	19	36	4	0	2
	M	2	1	2	2	1	0	0
	Subtotal	12	2	21	38	5	0	2
TOTAL		23	2	48	90	9	4	3

COMPARISONS OF ROOSTING CHARACTERISTICS OF *V. REGULUS* AND *N. GOULDI*

Vespadelus regulus selected roosts exclusively in hollows formed in trunks or branches of either dead standing trees (snags; 72%) or live marri and jarrah trees (28%). In contrast, *N. gouldi* showed a high versatility in the choice of roosts, roosting in spaces under exfoliating bark in both dead and live trees (44%), hollows (33%), cracks (15%) and even under balga

skirts (7%). One female *N. gouldi* roosted in a hollow of a burnt-out jarrah log (length = 7.48m; diameter = 56cm) on the ground for two consecutive days.

Both *V. regulus* and *N. gouldi* roosted in trees with a larger diameter (> 80 cm DBHOB) than random trees (Tables 4.3 and 4.4), but DBHOBs of both marri and jarrah trees used for roosting did not differ between bat species (Table 4.5). *V. regulus* selected taller jarrah trees for roosting than *N. gouldi* (Table 4.5), but there was no significant difference in mean height for marri roost trees between the two species. Even so, since a significant proportion of *V. regulus* roosts (n = 18) were in jarrah trees with only three roosts located in marri trees, it can be presumed that, in general, *V. regulus* selected significantly taller trees than *N. gouldi* (Table 4.5). Furthermore, the mean canopy height of roosting plots used by *V. regulus* was significantly greater than those used by *N. gouldi*, although the sites had similar canopy cover for both bat species (Table 4.5).

The two bat species also exhibited differences in roost heights. Even after excluding log and balga roosts, roost entrance heights of *N. gouldi* were significantly lower than those of *V. regulus* for both jarrah and marri tree roosts. Roost entrances of *N. gouldi* tended to be situated below the level of the canopy while those of *V. regulus* were within the canopy (Table 4.5).

ROOST CHARACTERISTICS

Based on tree and site variables, roost trees selected by both *V. regulus* and *N. gouldi* grouped separately from random trees in the MDS (Fig. 2). Marri and jarrah roosts used by *V. regulus* were greater in DBHOB and height compared to random trees (Table 3), and they were as tall as, or taller, than the forest canopy (t_{41} = - 0.26; P = 0.799). Furthermore, distances to the five

nearest available trees were significantly greater for jarrah roosts than for random trees (Table 3). However, marri roosts of *V. regulus* showed non-significant results for these variables, although the sample size was very small (n = 3). There were no significant differences in mean canopy height and mean canopy cover between roost plots of *V. regulus* and random plots for either tree species (Table 3).

Unlike *V. regulus*, roosting trees selected by *N. gouldi* had similar height to random trees (Table 4.4) but, relative to the overall canopy height, the roost trees were, on average, significantly shorter (t_{42} = -2.03; P = 0.048) (Table 4.4). This indicates that *N. gouldi* selected roosts within the sub-canopy. However, the mean DBHOB of both jarrah and marri trees used as roosts by *N. gouldi* were significantly greater than random trees (Table 4.4). The mean height of the nearest available trees was significantly less for jarrah roost trees than random trees, although marri roost trees did not show any differences. This was also true for mean canopy cover with jarrah roosts located in plots showing significantly less canopy cover than random locations, but no difference between marri roost plots and random locations (Table 4). Neither distances to the five nearest available trees nor mean canopy heights differed significantly between roost and random locations for either tree species (Table 4.4).

Both bat species displayed a clear preference for roosting in trees that contained >30% dead wood (Decay Stages 3 and 4; Table 4.1) while random trees, in comparison were all alive or < 30% dead (Decay Stages 1 and 2, Table 4.1). Roost trees were also, on average, at a more advanced stage of crown senescence, from moderate to advanced states of deterioration (Dead Branch Order; Table 4.1), compared with random trees (Tables 4.3 and 4.4). In addition, bats selected roosting trees with a bark cover of less than 25 percent (Bark Cover Classes 1, 2 and

3; Table 4.1), compared with random trees which had a bark cover of more than 25% (Bark Cover Class 4; Tables 4.3 and 4.4).

SELECTION OF ROOSTS AND LANDSCAPE FEATURES

Most roosts of *V. regulus* were in mature forest (*n* = 15; 71.4%), with the remainder in riparian buffers near ephemeral creek lines (*n* = 5; 23.8%) and a marked retained habitat tree in young regrowth forest (*n* = 1; 4.8%). No other *V. regulus* roosts were observed in young regrowth forest. As 95% of *V. regulus* roosts were in "mature forest", including riparian buffers, there was a significant preference for this forest type ($\chi^2 = 6.50$, $P < 0.011$), given that "mature forest" comprises approximately 80% of the study area (P. Collins, DEC, pers. comm.). By contrast, *N. gouldi* showed greater versatility in the location of roosts, selecting roosts in riparian buffers (*n* = 8; 29.6%), mature forest (*n* = 8; 29.6%) and remnant trees in shelterwoods (*n* = 10; 37.0%) as well as one large diameter tree in the gap release (*n* = 1; 3.7%). Based on the areal extent of these forest types, this species selectively roosted in shelterwood and gap forests that had been logged since 1985 ($\chi^2 = 28.65$, $P < 0.001$).The density of large diameter trees (DBHOB > 80 cm) with hollows and/or peeling bark differed significantly between forest treatments ($F_{4, 45} = 61.00$, $P < 0.001$). Riparian buffers had the highest density (21.6 ± 18.6 trees ha^{-1}), followed by mature forest (21.2 ± 18.3 trees ha^{-1}) and gap buffers (18.4 ± 15.8 $trees^{-ha}$), and there was no difference between these three treatments, but each had greater densities than either gap release (5.6 ± 4.9 trees ha^{-1}) or shelterwood creation silvicultural treatments (9.2 ± 7.9 trees ha^{-1}) ($P < 0.05$).

For *N. gouldi*, roost sites in both jarrah and marri were closer to the nearest water points than random plots (Table 4). In contrast, *V. regulus* did not show any preferences for roosting closer to water points, but its roosts were at lower elevations than random locations (Table 3).

There were only three inter-specific differences out of the eight landscape variables measured (Tables 1 and 5). *N. gouldi* roost sites in both jarrah and marri were significantly closer to water points than those of *V. regulus* (Table 5). For both tree species, *N. gouldi* also selected roosts closer to dams than *V. regulus* (Table 5). Lastly, *N. gouldi* roosts in marri were significantly closer to non-perennial watercourses than corresponding roosts of *V. regulus*.

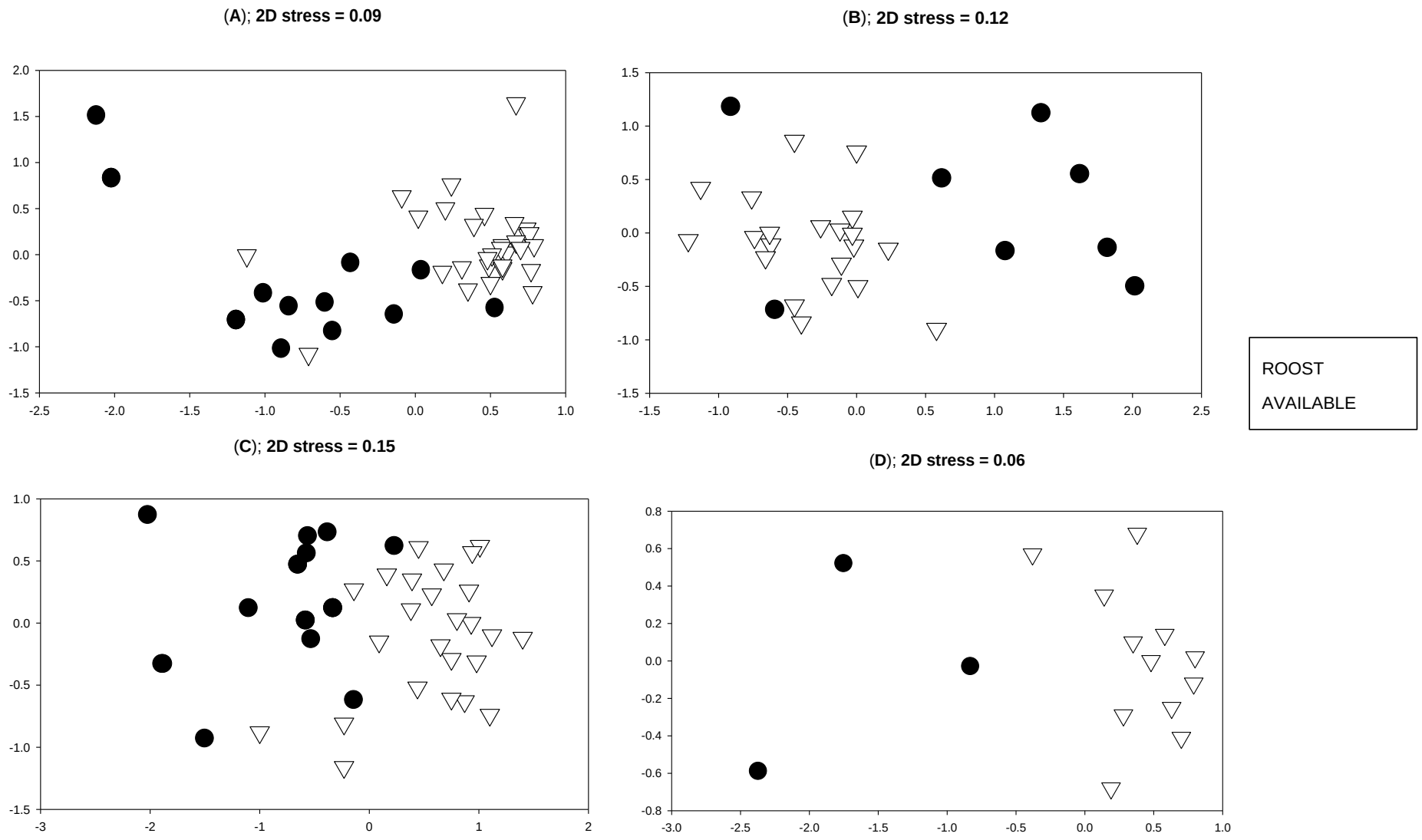

Fig. 4.2. Two-dimensional ordination (semi-strong hybrid multidimensional scaling ordination) based on measured variables of roost and random trees for *N. gouldi* [A (jarrah; ANOSIM Global test statistic, $R = 0.64$; $P = 0.001$); B (marri; ANOSIM Global test statistic, $R = 0.67$; $P = 0.001$)] and *V. regulus* [C (jarrah; ANOSIM Global test statistic, $R = 0.51$; $P = 0.001$) and D (marri; ANOSIM Global test statistic, $R = 0.94$; $P = 0.002$)].

Table 4.3. A comparison of continuous and ordinal variables for roost trees and plots of Southern forest bats (*Vespadelus regulus*) roosts with random trees and plots in the jarrah forests, south-western Australia, February – March 2009. Means (± S.E.) are presented, as are Mann-Whitney *U*-test results with associated probabilities. Significant results at $P = 0.05$ are shown in bold.

Variable	jarrah		marri		Mann-Whitney U-tests			
					jarrah		marri	
	Roost (n = 18)	Random (n = 25)	Roost (n = 3)	Random (n = 12)	$Z_{Adj.}$	P	$Z_{Adj.}$	P
Tree characteristics								
DBHOB (cm)	89.5 ± 7.4	41.1 ± 2.8	88.6 ± 21.2	33.5 ± 2.3	4.79	**<0.001**	2.62	**0.008**
tree height (m)	33.3 ± 1.3	27.3 ± 1.4	32.4 ± 3.3	23.1 ± 1.1	2.62	**0.009**	2.31	**0.021**
height relative to canopy height (%)	100.3 ± 3.9	85.0 ± 3.5	99.3 ± 5.4	79.3 ± 7.5	2.63	**0.008**	2.02	**0.043**
decay stage [a]	2.7 ± 0.2	1.4 ± 0.2	3.7 ± 0.3	1.3 ± 0.1	4.57	**<0.001**	2.95	**0.003**
bark-cover class [a]	3.7 ± 0.1	4.0 ± 0.0	3.0 ± 1.0	4.0 ± 0.0	-2.19	**0.028**	-2.00	**0.046**
crown senescence classification [a]	6.0 ± 0.5	2.8 ± 0.4	8.0 ± 1.5	2.0 ± 0.3	4.14	**<0.001**	2.60	**0.009**
Dead Branch Order (DBO) [a]	4.2 ± 0.3	2.7 ± 0.2	4.7 ± 0.3	2.1 ± 0.3	3.31	**<0.001**	2.60	**0.009**
Site characteristics (extrinsic variables)								
distance to nearest 5 available trees (m)	5.5 ± 0.3	4.1 ± 0.3	4.9 ± 1.3	5.0 ± 0.6	3.37	**<0.001**	-0.58	0.564
height of available nearest tree (m)	20.0 ± 1.4	25.1 ± 1.6	15.4 ± 3.0	21.5 ± 2.2	-2.19	**0.028**	-1.30	0.194
mean canopy height (m)	33.3 ± 0.7	32.0 ± 0.5	32.5 ± 1.6	30.4 ± 1.5	1.95	0.052	0.58	0.563
mean canopy cover	65.9 ± 2.1	68.2 ± 1.2	68.4 ± 8.3	67.3 ± 2.3	-0.15	0.883	0.00	1.000
Sub-canopy index	23.7 ± 1.9	42.0 ± 2.2	13.3 ± 2.7	32.4 ± 3.2	4.63	**<0.001**	2.46	**0.014**
Canopy index	30.8 ± 2.7	43.2 ± 1.6	30.0 ± 8.7	53.8 ± 5.0	3.51	**<0.001**	2.04	**0.041**
Landscape features [b]								
Slope (degree)	2.7 ± 0.4	2.7 ± 0.1	1.0 ± 0.0	1.4 ± 0.1	0.12	0.906	-1.48	0.139
Elevation (m)	207.0 ± 5.7	230.7 ± 3.1	199.7 ± 19.5	245.9 ± 4.2	-2.97	**0.003**	-2.05	**0.04**
Distance to nearest water point (m)	701.4 ± 48.5	704.4 ± 24.5	416.0 ± 225.7	537.7 ± 34.0	0.30	0.763	-0.57	0.570
Distance to perennial watercourses (m)	2100.7 ± 137.5	2382.9 ± 122.1	2152.6 ± 318.2	1476.1 ± 53.4	0.24	0.812	1.84	0.066
Distance to non-perennial watercourses (m)	248.5 ± 26.4	267.6 ± 13.7	173.8 ± 160.5	205.9 ± 13.3	-0.04	0.969	-0.73	0.467
Distance to nearest dams (m)	1960.4 ± 228.0	1980.5 ± 151.7	2350.4 ± 599.7	1915.6 ± 116.1	1.03	0.301	0.68	0.495
Distance to cleared land >10 ha (m)	486.8 ± 66.3	484.2 ± 31.6	360.9 ± 206.2	377.4 ± 22.2	0.52	0.603	-0.18	0.856
Distance to nearest gap or shelterwood	197.0 ± 35.8	180.8 ± 21.4	212.2 ± 42.7	210.2 ± 22.6	-0.18	0.780	0.43	0.665

[a] = Ordinal variables, all others are continuous

[b] = random jarrah trees (n = 118); random marri trees (n = 86). Roost trees are the same as at the local scale

Table 4.4. A comparison of continuous and ordinal variables for roost trees and plots of Gould's long-eared bat (*Nyctophilus gouldi*) roosts with random trees and plots in the jarrah forests, south-western Australia, February – March 2009. Means (± S.E.) are presented; as are Mann-Whitney *U*-test results with associated probabilities. Significant results at $P = 0.05$ are shown in bold.

Variable	jarrah		marri		Mann-Whitney U-tests			
					jarrah		marri	
	Roost (n = 14)	Random (n = 30)	Roost (n = 8)	Random (n = 21)	$Z_{Adj.}$	P	$Z_{Adj.}$	P
Tree characteristics (intrinsic variables)								
DBHOB (cm)	78.0 ± 7.4	34.8 ± 2.8	63.3 ± 8.9	40.1 ± 3.9	4.40	**<0.001**	2.36	**0.020**
tree height (m)	24.9 ± 3.2	26.3 ± 1.2	26.4 ± 3.5	26.0 ± 1.5	0.48	0.632	0.76	0.449
height relative to canopy height (%)	81.5 ± 10.5	88.6 ± 4.3	85.6 ± 9.9	92.0 ± 4.3	0.15	0.880	-0.54	0.591
decay stage [a]	3.2 ± 0.2	1.4 ± 0.1	3.3 ± 0.4	1.6 ± 0.1	4.82	**<0.001**	3.11	**0.002**
bark-cover class [a]	3.0 ± 0.2	4.0 ± 0.0	3.4 ± 0.3	4.0 ± 0.0	-4.81	**<0.001**	-3.42	**<0.001**
crown senescence classification [a]	6.8 ± 0.8	2.2 ± 0.2	6.3 ± 1.2	2.1 ± 0.3	4.47	**<0.001**	3.15	**0.002**
Dead Branch Order (DBO) [a]	4.6 ± 0.6	2.4 ± 0.2	5.0 ± 0.8	2.2 ± 0.2	3.19	**<0.001**	3.01	**0.003**
Site characteristics (extrinsic variables)								
distance to nearest 5 available trees (m)	5.4 ± 0.5	4.7 ± 0.3	5.2 ± 0.7	4.4 ± 0.5	1.18	0.236	1.02	0.305
height of available nearest tree (m)	23.2 ± 1.9	27.5 ± 1.6	24.4 ± 3.2	25.3 ± 1.6	-2.28	**0.023**	-0.15	0.884
mean canopy height (m)	30.6 ± 0.7	30.0 ± 0.7	30.3 ± 1.8	28.3 ± 1.0	0.43	0.668	1.20	0.232
mean canopy cover	60.8 ± 2.7	67.5 ± 1.3	64.8 ± 5.5	66.2 ± 2.1	-2.18	**0.029**	0.05	0.961
Sub-canopy index	33.4 ± 3.2	34.3 ± 1.7	31.0 ± 4.2	35.9 ± 1.9	-0.06	0.949	0.69	0.491
Canopy index	40.7 ± 2.9	46.0 ± 1.6	46.9 ±1.9	43.6 ± 1.8	1.53	0.126	-1.06	0.282
Landscape features [b]								
Slope (%)	3.36 ± 0.5	2.96 ± 0.1	4.0 ± 0.7	2.9 ± 0.2	0.84	0.402	1.70	0.090
Elevation (m)	221.1 ± 8.3	231.6 ± 3.2	241.8 ± 5.5	242.4 ± 4.4	-1.02	0.308	0.05	0.962
Distance to nearest water point (m)	492.3 ± 21.0	774.7 ± 32.6	608.4 ± 49.5	773.8 ± 32.3	-2.76	**0.006**	-2.41	**0.016**
Distance to perennial watercourses (m)	1734.2 ± 271.4	2382.9 ± 122.1	1237.2 ± 86.4	1476.1 ± 53.4	-1.32	0.188	-1.24	0.215
Distance to non-perennial watercourses (m)	262.4 ± 37.9	351.5 ± 18.1	216.0 ± 65.4	355.4 ± 24.2	-1.17	0.241	-1.53	0.126
Distance to nearest dams (m)	1379.6 ± 348.2	1980.5 ± 151.7	714.3 ± 53.4	1088.7 ± 84.8	-1.31	0.191	-1.36	0.173
Distance to cleared land >10 ha (m)	303.0 ± 41.0	484.2 ± 31.6	472.7 ± 61.1	470.5 ± 24.1	-1.57	0.117	-0.13	0.898
Distance to nearest gap or shelterwood	81.2 ± 19.5	74.2 ± 8.9	82.3 ± 17.8	75.2 ± 9.2	0.50	0.672	0.45	0.646

[a]= Ordinal variables, all others are continuous

[b] = random jarrah trees (n = 118); random marri trees (n = 86). The number of roost trees is the same as at the local scale

Table 4.5. Differences among continuous and ordinal variables between roosts that were used as roost sites by Southern forest bats (*Vespadelus regulus*; *n* = 10) and those used by Gould's long-eared bat (*Nyctophilus gouldi*; *n* = 11), at the focal-roost level and in the surrounding plots in the jarrah forests, south-western Australia, February – March 2009. Significant results are shown in bold.

Variable	jarrah		marri		Test statistic [a]			
	V. regulus (n = 18)	*N. gouldi* (n = 14)	*V. regulus* (n = 3)	*N. gouldi* (n = 8)	jarrah		marri	
					t_{30}	*P*	t_9	*P*
Tree characteristics								
DBHOB (cm)	89.5 ± 7.4	78.0 ± 7.4	88.6 ± 21.2	63.3 ± 8.9	-0.50	0.629	-1.19	0.252
tree height (m)	33.3 ± 1.3	26.8 ± 2.7	32.4 ± 3.3	26.4 ± 3.5	-2.10	**0.045**	-0.91	0.385
height relative to canopy height (%)	100.3 ± 3.9	87.7 ± 9.1	99.3 ± 5.4	85.6 ± 9.9	-1.59	0.122	-0.86	0.414
roost entrance height (m)	23.2 ± 1.2	11.5 ± 1.0	22.9 ± 2.2	12.7 ± 1.5	-6.49	**<0.001**	-2.63	**0.027**
decay stage [b]	2.7 ± 0.2	3.3 ± 0.2	3.7 ± 0.3	3.3 ± 0.4	-1.84	0.066	0.36	0.722
bark-cover class [b]	3.4 ± 0.1	3.0 ± 0.2	3.0 ± 1.0	3.4 ± 0.3	1.33	0.183	0.00	1.000
crown senescence classification [b]	6.0 ± 0.5	6.8 ± 0.8	8.0 ± 1.5	6.3 ± 1.2	-0.96	0.338	0.73	0.465
Dead Branch Order (DBO) [b]	4.2 ± 0.3	4.6 ± 0.6	4.7 ± 0.3	5.0 ± 0.8	-0.41	0.682	-0.32	0.752
Site characteristics (extrinsic variables)								
Mean distance to nearest 5 available trees (m)	5.5 ± 0.3	5.6 ± 0.5	4.9 ± 1.3	5.2 ± 0.7	-0.20	0.841	0.26	0.801
height of available nearest tree (m)	20.0 ± 1.2	24.4 ± 1.7	15.4 ± 3.0	24.4 ± 3.2	1.97	0.059	1.46	0.179
mean canopy height (m)	33.3 ± 0.7	30.5 ± 0.7	32.5 ± 1.6	30.3 ± 1.8	-2.59	**0.015**	-0.70	0.502
mean canopy cover	65.9 ± 2.1	60.8 ± 2.9	68.4 ± 8.3	64.8 ± 5.5	-1.44	0.160	-0.40	0.702
Sub-canopy index	24.2 ± 2.0	33.4 ± 3.4	13.3 ± 2.7	31.0 ± 4.2	2.39	**0.023**	2.85	**0.019**
Canopy index	31.7 ± 2.7	41.5 ± 3.0	30 ± 8.7	46.9 ± 1.9	2.06	**0.048**	2.88	**0.018**
Slope (degrees)	2.63 ± 0.5	3.36 ± 0.5	1.00 ± 0.00	4.00 ± 0.7	1.39	0.176	1.27	0.142
Elevation (m)	206.28 ± 7.1	221.07 ± 8.3	199.73 ± 19.5	241.76 ± 5.5	1.53	0.137	1.48	0.130
Distance to nearest water point (m)	711.38 ± 61.7	492.29 ± 30.0	608.00 ± 225.7	416.36 ± 49.5	-3.14	**0.004**	-4.12	**0.005**
Distance to perennial watercourses (m)	2131.24 ± 175.6	1734.16± 271.4	2152.57 ± 318.2	1237.19 ± 86.4	-1.92	0.065	-3.50	**0.007**
Distance to non-perennial watercourses (m)	256.75 ± 34.6	262.35 ± 37.9	173.84 ± 160.5	216.00 ± 65.4	0.26	0.796	1.42	0.106
Distance to nearest dams (m)	1988.64 ± 285.8	1379.56 ± 348.2	2350.42 ± 599.7	714.34 ± 53.4	-2.02	0.053	-5.39	**0.001**
Distance to cleared land >10 ha (m)	489.13 ± 82.4	303.01 ± 41.0	360.91 ± 206.2	472.67 ± 61.1	-1.27	0.215	1.54	0.157
Distance to nearest gap or shelterwood (m)	194.1 ± 43.1	83.6 ± 20.4	213.9 ± 44.9	81.6 ± 18.7	-1.12	0.274	-1.46	0.177

[a] = Two-sampled *t*-test, with comparisons for corresponding tree species, jarrah against jarrah (d.f. = 29) and marri against marri (d.f. = 9)
[b] = Ordinal variables, all others are continuous. Ordinal variables were compared using Mann-Whitney U-tests, with Z-adjusted as the test statistic

4.3 Discussion

ROOST AND SITE SELECTION

This is the first study to report on roost-site selection of bats in logged jarrah forests of south-western Australia. The data presented are, however, from a small number of observations on a small number of bats during late summer and autumn, outside the maternity season. For instance, bats were captured at only two water holes (Fig. 4.1b and c) and, therefore, it is possible that our observations may be influenced by the social behaviour of related individuals belonging to a social group. However, the influence of social behaviour may be minimal given that the bats were captured at two spatially distant waterholes located in areas with different logging histories at different times in February and March 2009. Moreover, our results share strong similarities to other studies of bat roosts in Australia, further suggesting that social behaviour did not strongly bias our results.

Despite the limitations of our data, this study revealed important and significant results in the choice of roost sites in a logged jarrah forest landscape in south-western Australia. Radio-tracked bats showed both inter-specific similarities and differences in the choice of roost trees and sites. While both bat species generally selected trees with large diameters, *V. regulus* roosted exclusively in hollows in tall trees, with 86% of all roosts occurring in jarrah and the rest in marri trees. This is consistent with other studies that have found a range of Australian bat species are dependant on *Eucalyptus* hollows (e.g. Lunney *et al*., 1985; Tidemann and Flavel, 1987; Taylor and Savva, 1988), including exclusive use of hollows as roosts by *Vespadelus pumilus* in *Eucalyptus* forests of northern NSW, Australia (Law and Anderson, 2000), and *Vespadelus vulturnus* within a remnant woodland on Phillip Island, Australia

(Campbell *et al*., 2005). Collectively this and other studies highlight the importance of tree cavities as roost sites for bats of the genus *Vespadelus* in Australia.

Compared to *V*. *regulus*, tree height was not an important factor for *N*. *gouldi*, which used a broader range of roost types including hollows, exfoliating bark, cracks and balga skirts. The use of many roost types by *N*. *gouldi* in this study is consistent with previous studies on *Nyctophilus geoffroyi*, which roosted in hollows, under bark, fissures, cracks, buildings, posts and hanging clothes (Tidemann and Flavel, 1987; Lumsden *et al*., 2002*a*). In contrast to our study, 75% of *N*. *gouldi* roosts were found in tree hollows in a logged forest in New South Wales, Australia (Lunney *et al*., 1988). The difference between the two studies could be due to the difference in the sampling period. Our study was conducted in February and March only, whereas Lunney *et al*. (1988) sampled bats over four different months, including the maternity season. Therefore, more observations on roost use throughout the year are required to comprehensively determine roost requirements for bats. Maternity roosts of *N*. *gouldi* and other Australian bats occur exclusively in tree hollows (e.g. Lunney *et al*., 1988; Law and Anderson, 2000), which likely partly explains the differences between the two studies. Therefore, more observations on roost use throughout the year are required to comprehensively determine roost requirements for bats, but we consider it likely that tree hollows are a critical resource for *N*. *gouldi*, particularly as maternity roosts.

Bats of both species selected trees with a mean DBHOB > 80 cm, which is consistent with those reported for other Australian bats (e.g. Lunney *et al*., 1988; Herr and Klomp, 1999; Law and Anderson, 2000; Lumsden *et al*., 2002*a*) and, as reported by

many studies elsewhere, roost trees were significantly larger than random trees. These findings add to available evidence that older and large mature trees are important roost sites for bats (e.g. Sedgeley and O'Donnell, 1999; Lumsden *et al*., 2002*a*; Kalcounis-Rüppell *et al*., 2006). In addition, both species frequently used roosts in trees at intermediate or advanced stages of decay, crown senescence and deterioration with a lower percent bark cover than random trees. Larger trees generally contain larger and more hollows (e.g. Gibbons *et al*., 2000; Whitford and Williams, 2002) and potentially thicker decorticating bark with better thermal properties that offer better protection from inclement weather and predators (Sedgeley, 2001; Kunz and Lumsden, 2003). However, Turbill (2006) found male *Nyctophilus gouldi* can save energy by roosting in exposed locations under bark and using passive warming from solar radiation to arouse themselves from torpor, which may explain their reduced reliance on hollows in this study.

We found inter-specific differences in the choice of roost sites with respect to vegetation structure and canopy cover. While *N. gouldi* selected roosts closer to vegetation with a higher canopy cover, *V. regulus* roosts were located in more open habitat with less canopy cover. In addition, hollow entrances of *V. regulus* were high (≥ 22 m) above ground. In contrast, roost entrances of *N. gouldi* were within 13 m above ground and the species tended to locate roosts in structurally complex and cluttered vegetation with higher overstorey tree densities and more midstorey and understorey trees than *V. regulus* (Table 4.5). Mature forest and unlogged buffers in this study were relatively open and had less understorey and mid-story vegetation compared to the more closed and dense young regrowth. The differences between the two bat species in the choice of roost sites with respect to roost entrance height and

closeness to vegetation may have been due to their differential levels of clutter tolerance (Table 4.5). *N. gouldi* is typically a clutter tolerant species because of its low aspect ratio and wing loading that allows slow flight and high manoeuvrability in dense vegetation (Fullard *et al*., 1991). In contrast, *V. regulus* bats have an intermediate aspect ratio and wing-loading and are not well adapted for highly manoeuvrable flight (O'Neill and Taylor, 1986). This may explain their preference for roosting in the more open mature forest and riparian buffers, while avoiding the more closed, dense young regrowth. Open forest may also be favoured for roosting because its structure allows more direct sunlight on tree trunks and canopies, which may confer thermal advantages for developing young (Racey and Swift, 1981; Turbill and Geiser, 2005). Alternatively, the more open forest conditions could be an indicator of forest age, with mature forest providing more roosting opportunities resulting from many large diameter trees with more hollows.

MATURE FOREST AND RIPARIAN BUFFERS AS ROOST SITES FOR BATS

Both species relied heavily on buffers for roosting, although *V. regulus* roosted further from creek lines than *N. gouldi*. Buffers were contemporarily unharvested forests (i.e. > 30 years unlogged, and lightly selectively harvested when previously done so) retained adjacent to gap release cells (i.e. TEAS – temporary exclusion area system) and around ephemeral drainage lines and streams (i.e. riparian zones). Therefore the use of these areas was likely due to their structure and placement in the landscape rather than the presence of water (Perry *et al*., 2007). The location of 95% of roosts used by *V. regulus* in mature forest and buffers during this study was significantly greater than was randomly available within the study area, indicating a strong

preference for these stands. In contrast, *N. gouldi* appeared to prefer forests that have been logged since 1985.

As in other studies, individual bats of both species changed roosts often, moving to a new roost every 1 – 2 days, but displayed fidelity to a general area. Bats of both species generally preferred roosting in older forest, probably because these forests provided sufficient alternate roosts required for long-term use (Lumsden *et al*., 2002*a*). The mature and/or uncut forest contained a much higher density of trees with hollows (16 – 32 trees ha^{-1}) compared to shelterwood creation and gap release sites (8 – 12 trees ha^{-1}). Mature forest hollow densities are comparable to the average densities of live and dead hollow trees of 17 ha^{-1} and 18 ha^{-1} for *Chalinolobus gouldii* and *Nyctophilus geoffroyi* roost areas, respectively, in a fragmented landscape in south-eastern Australia (Lumsden *et al*., 2002*b*), while the densities in the shelterwood and gap release stands were similar to the 11 ha^{-1} in 'available habitat' where these bats were not found to roost in the same study in south-eastern Australia (Lumsden *et al*., 2002*b*). These results are consistent with other studies that found most bats prefer older forest stands or mature forests in Australia (e.g. Lunney *et al*., 1988; Taylor and Savva, 1988; Law and Anderson, 2000; Lumsden *et al*., 2002*a*), and elsewhere in temperate forests (e.g. Brigham *et al*., 1997; Crampton and Barclay, 1998; Sedgeley and O'Donnell, 1999). However, where older forest is absent, *Vespadelus pumilus* maintains similar colony sizes in the scarce roosts remaining within regrowth forest (Law and Anderson, 2000). At present, it is unknown what roosts would be used by jarrah forest bats in areas where mature forest is locally scarce.

N. gouldi selected roosts closer to water holes than was randomly expected. The water holes are typically artificial water points, used as water sources for fire suppression, and were distributed throughout the forest. Two factors might explain the bats' preference for roosting closer to water holes. First, it would reduce the time and energy spent commuting to the water points for drinking and/or foraging for insect prey over water (Lewis, 1995; Kunz and Lumsden, 2003; Fukui *et al*., 2006). Secondly, being lower in the landscape, these areas generally coincided with riparian buffers, which contained many large diameter trees with hollows hence greater roosting opportunities.

The two bat species used retained habitat trees in gap release and shelterwood creation silvicultural treatments as roost sites, but this was very infrequent in *V. regulus*. Further studies are required to demonstrate if these retained trees can be used effectively by viable populations of bats, especially in the absence of unlogged mature forest and riparian buffers, but our results suggest this would be unlikely, at least for *V. regulus*. Given the dependence of jarrah forest bats on tree hollows as maternity roosts, studies examining the use of retained habitat trees as roosts during the maternity season are important in understanding the value of retained trees in helping maintain bat populations in production forests.

Current guidelines for jarrah forest harvesting involve retention of 5 primary habitat trees ha^{-1} and 6-8 secondary habitat trees ha^{-1} in areas cut to gap, shelterwood or 'selective cut in dieback' (CCWA, 2004). Between 1996 and 2003 there were provisions for 4 primary habitat trees plus 6-8 secondary habitat trees (if present) (Silviculture Guideline 1/95). Prior to this it was 15 trees per 5 hectares (Silviculture

specification 5/89). While these improvements in the number of retained, actual and potential, habitat trees are important for the long-term maintenance of roost sites for bats in logged jarrah forests, it is unclear whether these measures are sufficient in themselves and, therefore, should be a subject for future studies, as discussed above. Indeed, they are much lower than the hollow tree density reported by Lumsden *et al*. (2002*b*) in a fragmented landscape in south-eastern Australia, but they are similar to densities in a regrowth forest growing on lower slopes in northern NSW (Law and Anderson, 2000). Although the retention and sustained recruitment of large mature trees at various stages of decay in logged forests is essential for the long-term maintenance of roost sites for bats and other hollow-dependent fauna into the future, the presence of retained habitat (e.g. fauna habitat zones, unlogged buffers and old growth forest) appears more important, indicating that a consideration of habitat provisions and availability at a landscape scale is crucial.

The logging rotation in the jarrah forests is dependent on a 10-year forest management plan (FMP), with the current FMP ending in 2014. At two forest blocks, Kingston and Warrup, where our study was undertaken, approximately 54% of the total area (11,740 ha) is currently reserved from logging as conservation reserves, informal reserves (riparian buffers, diverse ecotype zones, road reserves), old growth forest, and fauna habitat zones. Of these, only about 39% are permanently reserved (including riparian buffers) from logging in the future. Most of the study area had experienced at least one cycle of harvesting between the 1920s and 1979, typically in a selective manner that still retained many mature elements of the original forest. Currently, at least 6% has no evidence of being previously cut and since 1980; approximately 20% of the study area has been harvested, generally for the second

time. The remaining 26% of the study area available for harvesting may potentially be harvested in coming decades, in addition to follow-up silvicultural treatment in the post 1980 harvest areas (CCWA, 2004). Many forest areas outside the study area may reflect this trend. Thus, many forest areas may have already been selectively logged, and with increasing pressure on remaining areas of forest that will be logged during the second rotation, it is uncertain whether jarrah forest logging will retain sufficient habitat containing multiple old hollow-bearing trees required for many roosting bat species and other hollow-nesting fauna.

CONCLUSIONS

Our study reveals some important implications for the management of bat roost sites. The two bat species chose different roosts with respect to the level of clutter, height and location in the landscape. While *N. gouldi* selected roosts at sites with more clutter, *V. regulus* roosts were located in open areas of mature forest and riparian buffers. Although gap release and shelterwood creation sites retained tall and large diameter hollow-bearing trees that were less cluttered than surrounding vegetation, it seems at least *V. regulus* avoided locating roosts in such treatments when older forest was available nearby. In general, remnant trees, including retained habitat trees, in these silvicultural treatments were not preferred by bats, especially *V. regulus*, as roost sites during late summer and early autumn and further studies are required to investigate if they are used successfully by breeding bats when old forest is absent or less accessible. Given the high rates of roost switching and the variety of roost sites used by bats, it is essential that multiple roosts are maintained and continually recruited in the forest to satisfy bat roosting requirements (Willis and Brigham, 2004; Russo *et al*., 2005).

Our study demonstrated the importance of unharvested buffers surrounding ephemeral streams, and more open mature forests, with relatively open understoreys, as roosting habitats for both *V. regulus* and *N. gouldi*, probably because they provided a large pool of older and mature trees in a variety of decay classes as roost sites. In this regard, provisions since 2004 for Fauna Habitat Zones (i.e. >200 ha areas with mature forest structure generally interspersed 2-4 km apart within areas available for logging (CCWA, 2004, FMP 2004-2013) are likely to benefit bats, particularly those that rely on blocks of forest that maintain mature forest attributes or characteristics. Notably, our study provides only a snapshot of bat habitat use and preferences. Serious management consideration should also be given to foraging habitat, and overwintering and maternity roost sites (Sedgeley, 2001; Kunz and Lumsden, 2003; Lumsden *et al*., 2002*a*). While logging impacts on bat activity including foraging activity is examined elsewhere (**Chapter 3, Webala *et al*...*in press***), targeted research on temporal/seasonal differences in roost use needs to be undertaken in the jarrah forests of south-western Australia.

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Chapter 5

General discussion: Bat general habitat use in logged jarrah forests and its implications for management

Plate 5.1. Jarrah roost tree for southern forest bat (*Vespadelus regulus*).

There is a general lack of understanding of the habitat requirements of many wildlife species in Australia, and uncertainty about the effectiveness of current management strategies involving ecologically sustainable forest management at providing suitable habitat in timber production forests. While a reasonable amount of information exists

about the effects of forest loss and modification on fauna (e.g. Abbott and Whitford, 2002; Whitford and Williams, 2002; Wardell-Johnson *et al*., 2004; Whitford and Stoneman, 2004), there are some taxa, such as bats, where logging impacts are poorly understood (Law, 1996). It is especially important to have this information for forest dependent bats, and the modified and fragmented post-logging forest habitats must adapt if these bats are to be conserved. Many of these species are hollow-dependent, but there is a general dearth of information on hollow use and availability and foraging requirements for these species in Australia (Gibbons and Lindenmayer, 2002).

In the jarrah forests of south-western Australia, many animals, such as possums, phascogales, cockatoos and bats require hollows for shelter and to breed. As thousands of hectares of jarrah forest are logged every year, old growth forests, which contain relatively large, old trees and habitat features, such as hollows, dead standing trees and logs, will disappear. While short-term impacts on arboreal mammals, birds and insects have been examined in the jarrah forests (e.g. Abbott *et al*., 2003; Rhind, 2004; Craig and Roberts, 2005; Wayne *et al*., 2006), nothing is known about logging impacts on bats and whether ESFM is successful in maintaining bat populations in logged areas.

This thesis contributes information that will increase the understanding of habitat requirements of forest dependent bats and the effectiveness of current management practices in timber production forests in maintaining bat populations. Firstly, it has gathered information on the general habitat use of logged landscapes. Specifically, the thesis reveals information on post-logging effects on the activity of individual species,

and the community, of jarrah forest-dwelling bats. Secondly, the thesis also provides information on the availability and use of fauna nesting sites, such as tree hollows, by investigating impacts of logging on the roosting requirements of two sympatric species of jarrah forest-dwelling vespertilionid bats, the southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi* and the effectiveness of current management practices at conserving appropriate roost sites.

This final chapter synthesises the main results in chapters 3 and 4, followed by a discussion on the implications for the conservation of bats and other forest dependent fauna in logged forests. In particular, the importance of structurally mature forest, unlogged buffers and trees retained as part of current management measures are discussed.

This thesis revealed some important information for the conservation of bats and other forest dependent fauna in forests managed for both timber production and biodiversity conservation. **Chapter 3** demonstrated that forest tracks, rather than logging history, had greater influence on bat habitat use, including foraging. Therefore, the extent of logging impacts on bats was less in the short term and this is largely because bats are able to tolerate some level of landscape modification because of their high mobility (Kalko *et al*., 1999; Medellín *et al.*, 2000; Rhodes and Wardell-Johnson, 2006). Although most species in this study avoided the interior of regrowth forest, due to dense clutter, they were able to utilize logged forest areas using tracks, highlighting the key role of forest tracks in maintaining bat activity within post-disturbance forests, especially regrowth forests. Forest tracks provide linear edges of lower clutter, which assist in maintaining high bat activity in regrowth forest areas (Law and Chidel, 2002;

Lloyd *et al*., 2006). However, tracks represent a small proportion of the forest landscape, and therefore additional measures are required to maintain viable populations of bat species in selectively logged forests (Law and Chidel, 2002; Lloyd *et al*., 2006). This study, nonetheless, demonstrates that tracks cutting across the forest landscape facilitate use by many commuting and foraging bat species in otherwise cluttered young regrowth forest, and have the potential to ameliorate logging impacts in selectively timber-harvested forests (Law & Chidel 2002; Lloyd *et al*., 2006).

Changes to jarrah forest logging practices over the last two decades have seen a shift to ecologically sustainable forest management (ESFM) (Lindenmayer, 1999; Calver and Wardell-Johnson, 2004). ESFM measures include the retention of unlogged patches/buffers of vegetation (between logged coupes and along riparian buffers) to assist in maintaining native habitat for flora and fauna, and the retention of habitat trees within net (actual) logged areas (CCWA, 2003). In comparison to forest tracks, unlogged buffers constitute a much greater proportion of the jarrah forest landscape, and were potentially better at ameliorating logging impacts on bats in this study. Firstly, they provided abundant insect prey in areas of relatively reduced clutter for foraging bats. Secondly, and most importantly, they provided multiple roosting opportunities for bats because they contained a higher density of old hollow-bearing trees than other post-logging forest silvicultural treatments (see below). These measures should increase open spaces and edges required by many foraging bat species (Law and Chidel, 2002). Other prescriptions such as temporary exclusion areas, fauna habitat zones and informal reserves and the protection of old-growth forests are likely to be important in providing areas of relatively low or moderate

clutter. Together, these prescriptions create a mosaic of informal reserves entrenched within logged landscapes, which should serve as an ameliorative measure for bat activity against logging impacts. However, it is unclear to what extent jarrah forest logging could be causing bat population declines, and therefore banding of bats to estimate population sizes should be a priority for future studies.

While many bat species in this study foraged in regrowth areas, especially on forest tracks, radio-tracked bats avoided locating roosts in young regrowth forests (**Chapter 4)**. Indeed, most bat roosts were located in hollows of old, large mature trees in either structurally mature forest or unlogged riparian buffers. Their preferences for mature forest and unlogged streamside buffers over regenerating forest after harvest suggests that bats used retained areas (i.e. the unlogged riparian buffers and mature forest) for both foraging and roosting, and regrowth forest for foraging only, implying that in modified landscapes, such as the logged south-western Australian jarrah forests, roost availability is likely to be the ultimate factor determining the persistence of bat populations. Thus, this study lends credence to reviews suggesting that roost-site destruction is one of the major factors contributing to the decline of bats in many parts of the world, even when suitable foraging habitat is widely available (Kunz and Lumsden, 2003; Kalcounis-Rüppell *et al*., 2006).

Many hollow-dependent bats are known to switch roosts almost on a daily basis but the roosts are in the same general area (Lunney *et al.,* 1988; Lunney *et al*., 1995; Kosken, 1996; O'Donnell and Sedgeley, 1999; Law and Anderson, 2000; Lumsden *et al*., 2002*a*; Kunz and Lumsden, 2003). Roost switching may be necessary for a number of reasons, including a reduction in predation risks, decrease in commuting

costs to foraging areas, minimise parasite loads and a search for roosts with the right microclimatic conditions (O'Donnell and Sedgeley, 1999; Sedgeley and O'Donnell, 1999*a*; Sedgeley, 2001; Kunz and Lumsden, 2003). That the majority of bat roosts occurred in structurally mature forests and riparian buffers in this study could be attributed to the fact that these sites contained high densities of old, large trees with hollows, which enabled roost switching, as compared to gap release and shelterwood creation silvicultural treatments, which had much lower densities of hollow-bearing trees. Conversely, although gap release and shelterwood creation sites retained tall and large diameter trees that were less cluttered than surrounding vegetation, there was little evidence to show that bats used roosts in these silvicultural treatments during summer and autumn. In particular, *V. regulus* avoided locating roosts in such treatments when older forest was available nearby. Exactly why bats avoid roosting in remnant or retained habitat trees in regrowth forests is unclear but two factors may be important. Firstly, bats preferred hollow trees in mature forest and unlogged riparian buffers because these areas contained multiple hollow bearing trees for bats to switch roosts frequently. In contrast, insufficient tree hollows were available in young regrowth for roosts to be switched as frequently as required. Secondly, mature forests and riparian buffers also contained abundant insect prey in vegetation less cluttered than regrowth areas and, therefore, provided the best foraging habitat for bats. Consequently, bats may have selected roosts closer to these good foraging sites to minimize energetically costly commuting distance (Kunz and Lumsden, 2003), as the two species studied have small ranges. Further studies are needed to determine which of these factors is the most important determinant of roost site selection and also to determine whether breeding bat populations can successfully use regrowth forests in the absence, or inaccessibility, of mature or old-growth forests. This study highlights

the importance of mature forest and unlogged buffers as bat roost sites in logged jarrah forests of south-western Australia, but the area of old growth forest required by these and co-occurring bat species remains to be determined. Nonetheless, the retention of habitat trees may mitigate against logging impacts on bats and other hollow-dependent fauna in the long term. ESFM prescriptions should therefore aim to ensure the perpetuation of a minimum density of hollow-bearing trees in harvested areas (at least 16–32 trees ha^{-1}) and, where possible, the density of retained habitat trees should be increased. Retained trees are likely to have a large impact on the population viability of bats and other hollow-dependent fauna, especially where unlogged buffers are absent or too small in area.

This study demonstrated the importance of retained unharvested buffers surrounding ephemeral streams, with typically open understoreys, as roosting habitats for bats, probably because they provided a large pool of older and mature trees, in a variety of decay classes, as roost sites. Although many bats are able to forage further away from roost sites due to their flight mobility (e.g. Lumsden *et al*., 2002*a*), they need hollows for roosting (e.g. this study, Law and Anderson, 2000). During the breeding season, the capacity of lactating females to range widely in search of food is counterposed against the need to return regularly to warm and feed juveniles. Riparian buffers therefore allow bats, especially lactating females, to forage closer to roosting sites. As reported elsewhere, these low-lying areas are important as roosting sites for bats (e.g. Lunney *et al*., 1988, Taylor and Savva, 1988; Law and Anderson, 2000; Schulz, 2000) and should be protected for the conservation of bats and other hollow-dependent fauna in logged forests.

As in other studies, this study showed that bats were highly selective in choosing roost sites. Compared to random trees, trees chosen for roosting were older and larger (> 80 cm DBHOB) at intermediate or advanced stages of decay and crown senescence and with a lower percent bark cover. These findings add to available evidence that old and large mature trees are important roost sites for bats (e.g. Lunney *et al*., 1988; Taylor and Savva, 1988; Herr & Klomp, 1999; Sedgeley and O'Donnell, 1999b; Law & Anderson, 2000; Lumsden *et al*., 2002*a*; Kalcounis-Ru¨ppell, Psyllakis & Brigham 2006), having existed long enough for hollow formation (Mackowski, 1984; Gibbons *et al*., 2000; Lindenmayer *et al*., 2002; Whitford, 2002; Smith *et al*., 2008). This suggests that forests lacking trees large enough to contain these hollows will provide fewer roosting opportunities and this could affect the abundance and diversity of bats. Furthemore, in forests managed for timber production, silvicultural practices are likely to greatly reduce the density of hollow-bearing trees, especially where repeated harvesting events occur (Lindenmayer *et al*., 1991; Smith *et al*., 1994; Ross, 1999). In addition to maintaining a representative reserve system, it is crucial to manage non-reserved areas to ensure that sufficient habitat elements are protected and maintained into the future. This study showed that when properly implemented, buffers of unlogged forests can act to mitigate logging impacts on fauna through the provision of roosting habitat for bats. With approximately 39% of the total area of forest in the study area currently reserved from logging in the foreseeable future (CCWA, 2004), it is unclear to what extent continued harvesting in the jarrah forests will compromise the viability of bat populations in the future. Addressing the extent to which logging operations impact on the density of hollow-bearing trees should be a priority for future research.

The harvest rotation cycles (i.e. interval between the harvests of mature forest through to the maturation of the subsequent regrowth) in jarrah forest range from 100 -200 years. In accordance with the principles of phased cutting cycles, temporarily excluded areas adjacent to previously harvested patches (buffers) may themselves become available for harvest from 10 - 20 years after the initial harvest (CCWA, 2004). These rotation intervals between harvesting events in the jarrah forest may be insufficient to allow for hollow development and will have a negative effect on the survival of jarrah forest-dwelling bats (Recher, 1996; Gibbons and Lindenmayer, 1996). With short harvest rotation cycles and the lack of evidence for the use of retained habitat trees in regrowth forests, the unlogged riparian buffers and other areas of jarrah forest that will remain unlogged in the future become critical habitat for bat conservation, especially as they provide key roosting habitat. This study recommends that logging rotations be lengthened to allow for the forest to at least attain mature forest elements, such as tree hollows suitable for occupation by wildlife, which may take several hundred years to develop (Mackowski, 1984; Gibbons *et al*., 2000; Lindenmayer *et al*., 2002; Whitford, 2002; Smith *et al*., 2008) until conclusive evidence becomes available that logging gap buffers at the second rotation does not negatively impact on bat populations.

General conclusions

Logging programmes as currently operating in the south-western Australian jarrah forests, create a mix of tree age classes, providing a mosaic of forest patches with different structures. Jarrah forest logging creates patches of different aged logging regrowth with patches of unlogged buffers, retained trees and other features such as old growth forest incorporated into the larger logged landscape. While timber

harvesting has short-term impacts on wildlife, many species of flora and fauna can progressively recolonise logged sites as the forest regenerates. For instance, in this study, foraging bats avoided interior regrowth forest but had access nonetheless on tracks. Logging can, however, also have longer-term impacts on birds and mammals that use tree hollows as nesting and breeding sites. Habitat retention, as provided by adjacent streamside buffers and (previously lightly logged) mature forest in the jarrah forests were important roost sites for bats, and could mitigate against logging impacts in the long term. This study principally identified the value of structurally mature jarrah forest and large old trees as roosting sites for bats, and these should be protected as a safe haven for many old-growth dependent faunal species.

Provisions since 2004 for Fauna Habitat Zones (i.e. >200 ha areas with mature forest structure generally interspersed 2-4 km apart within areas available for logging (CCWA, 2004, FMP 2004-1013) are likely to benefit bats and other fauna that rely on mature forest attributes or characteristics. Although Law and Anderson (2000) found that *Vespadelus pumilus* bats used regrowth forest for both foraging and roosting in northern New South Wales, Australia, retained habitat trees in logged coupes were avoided by roosting bats in this study and further studies are required to demonstrate if these can be used effectively by viable populations of bats, especially in the absence of mature unlogged forest and unlogged riparian buffers. In addition, further research is required to shed light on bat overwintering and maternity roost sites that are important for the survival of bat populations (Sedgeley, 2001; Kunz and Lumsden, 2003; Lumsden *et al*., 2002*a*) . Elsewhere, studies report that many bats are highly selective of roost sites during the breeding season, with maternity roosts located in large old trees in mature, and unlogged streamside, forests (e.g. Lunney *et al*., 1988,

Brigham *et al*., 1997; Law and Anderson, 2000; Lumsden *et al*., 2002*b*). Therefore, maternity roosts of jarrah forest bats would most likely occur in mature forests and unlogged riparian buffers and these should be maintained for the conservation of bats and other fauna requiring mature forest elements such as hollows in large old trees for nesting. In addition, a long-term study to clarify temporal/seasonal and intra-specific variation in bat distribution and roost site selection needs to be undertaken in the jarrah forests of south-western Australia to better determine if current ESFM practices are effective at maintaining bat populations in logged forests.

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